Paddlefish movements and habitat use in Pool 13 of the Upper Mississippi River during low water conditions

by

Clark Thomas Moen

A Thesis Submitted to the
Graduate Faculty in Partial Fulfillment of the
Requirements for the Degree of
MASTER OF SCIENCE

Department: Animal Ecology
Major: Fisheries Biology

Signatures have been redacted for privacy

Iowa State University
Ames, Iowa
1989

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

A radio-telemetry study of adult paddlefish was conducted in Pool 13 of the Upper Mississippi River during 1988 to assess movements and habitat use during unusually low water conditions. For March to August, mean monthly discharges of Lock and Dam 12 averaged 42% below the 47-year means. Thirty-five large fish received radio implants and 32 fish provided data on movement and habitat use. Individual fish were located 812 times in 1988; 774 contacts were made in Pool 13 during spring and summer. No tagged paddlefish moved upstream from Pool 13, but six fish moved through Lock and Dam 13 into Pool 14 between June and November, 1988.

Most paddlefish exhibited a random pattern of movement, and the direction of movement was not explained by changes in river stage or discharge, even during spring. Rates of movement were not significantly different between males and females, but the linear range for females was twice that for males. The greatest linear distance moved by a radio-tagged paddlefish was 92 km downstream and the greatest cumulative movement was 435 km, entirely within Pool 13.

Nearly three-fourths of all contacts with paddlefish occurred in about 5% of the available habitat in Pool 13. The tailwaters below Lock and Dam 12 were strongly preferred

by paddlefish during spring and summer 1988, and spring 1989, when the gates were fully opened and fish could have moved upstream. Main channel borders with wing dams were also strongly preferred. Males were located more frequently in the tailwaters than females, especially during summer.

Backwater areas and side channels were largely avoided by paddlefish. However, more than two-thirds of all contacts were made in the tailwaters and in main channel borders with wing dams located near the mouths of backwater areas. Unlike in an earlier study (1982), paddlefish were also found in the most lacustrine area of the pool. At locations where tagged paddlefish were encountered, depths were generally greater and water temperatures higher than the present Habitat Suitability Index models consider optimal. It is concluded that the tagged fish moved randomly within the pool and that, under drought conditions, the tailwater area and the deeper scour holes near the entrances to backwaters were extremely important to paddlefish.

INTRODUCTION

The paddlefish, Polyodon spathula (Walbaum), is an ancient, mainly cartilaginous fish that has fossil ancestors as far back as the Cretaceous Period, 120 million years B. P. (MacAlpin 1947; Lagler et al. 1977; Carlson et al. 1982). It is the sole North American representative of the Family Polyodontidae. The paddlefish is a long-lived species (up to 30 years (Purkett 1963)) that inhabits large-river systems and feeds primarily on zooplankton (Meyer 1960; Rosen 1976; Rosen and Hales 1981), immature insects (Wagner 1908; Eddy and Simer 1929; Hoopes 1960; Meyer 1960),and, occasionally, small fish (Fitz 1966).

The paddlefish is one of North America's largest freshwater fishes. The largest one on record was speared in Iowa's Lake Okoboji in 1916 and was about 2.2 m in length (Nichols 1916) and weighed over 90 kg (Harlan and Speaker 1956). During their first year of life, paddlefish growth is typically rapid (Russell 1986). For example, young-of-the-year paddlefish hatched during early May in Oklahoma grew in length by 4.3 mm/day during summer, and attained a mean length of 72 cm by December (Houser and Bross 1959). The growth rate is largely dependent on the abundance of zooplankton (Russell 1986).

Evidence from several localities indicates that female paddlefish mature later in life, spawn less frequently, and may live longer than males (Scarnecchia et al. 1990). Male paddlefish typically mature at seven to nine years of age at a length of one meter and 7.9 kg and females at ages 10 to 12 at a length of 1.3 m and 13.6 kg (Russell 1986; Gengerke 1986). Russell (1986) suggests that males spawn annually, but females, which may produce more than one million eggs, may require two or more years between spawns. Paddlefish often migrate long distances in the spring to reach their spawning grounds. For example, paddlefish in the Yellowstone River (Montana) have moved 160 km over an interval as short as 17 days (Rehwinkel 1978).

Paddlefish originally were distributed throughout the Mississippi River and adjacent Gulf Coast drainages (Hubert et al. 1984). In the early 1900s, paddlefish were distributed as far as the Great Lakes (Carlson and Bonislawsky 1981), and Ontario, Canada (Burr 1980). In the last 100 years, however, paddlefish abundance has decreased throughout the historical range, especially along the periphery. Paddlefish have been extirpated from four states and Canada (Gengerke 1986), and nine of the 22 states with paddlefish populations have reported declines in those populations (Unkenholz 1986). The primary causes of these declines have been excessive harvest and human alteration of the paddlefish's large-river habitats.

According to Pasch and Alexander (1986), exploitation has never been the sole cause of a severe decline in a paddlefish population, but has been an important contributing factor in several specific cases. Commercial exploitation of paddlefish stocks began around 1900, when the depletion of lake sturgeon (Acipenser fulvescens) stocks resulted in a need for an alternative source of caviar (Carlson and Bonislawsky 1981). During the early commercial fisheries on the Upper Mississippi River (UMR: from the headwaters in northern Minnesota to Cairo, Illinois; Rasmussen 1979), paddlefish were the most sought-after commercial fish species (Evermann 1902). U. S. commercial harvest peaked in 1899 at 1,094 metric tons and had declined by 60% to 426 metric tons by 1975 (Gengerke 1986). In the UMR, only Illinois allows commercial fishing for paddlefish as of 1989. With the recent increase in roe value to as much as $88/kg -- making a large gravid female worth $200 or more for her roe alone (Russell 1986) -- there is additional incentive for excessive harvest. In addition to the commercial fisheries, significant recreational fisheries based on snagging have developed in numerous localities, especially in the tailwaters of dams where fish are often concentrated.

Habitat alterations have been primarily responsible for the decline of many paddlefish stocks (Pflieger 1975; Carlson and Bonislawsky 1981; Unkenholz 1986). Point- and non-point-source pollution, erosion, construction of water control structures, dredging, and channelization have reduced the quantity and quality of habitat for paddlefish (Sparrowe 1986). Pollution and erosion have resulted in siltation and poorer water quality. Water control structures have altered natural river flows and impeded or prevented upstream spawning migrations by paddlefish (Russell 1986).

Before impoundment of the major tributaries in the Mississippi Valley, extensive natural backwater areas, oxbow lakes, and braided channels existed (Russell 1986). Adult paddlefish were evidently most frequently found in these areas of slower currents (Stockard 1907; Wagner 1908; Coker 1930; Rosen 1976). Wagner (1908) noted that paddlefish were often found in large schools in backwaters, feeding on the abundant zooplankton while expending relatively little energy. In many cases, when the tributaries were dammed, additional quiet-water habitat was created by the inundation of lowlands. According to Rosen (1976) and Southall and Hubert (1984), quiet or nonflowing habitats are important to paddlefish as food-producing areas. Paddlefish are frequently found in close proximity to the main channel and are associated with islands, sand bars, and other man-made or natural obstructions that reduce the current velocity from that in the main channel (Rosen et al. 1982; Southall and Hubert 1984). Since the adults are quite mobile, Thompson (1933) suggested that they use several habitat types.

The known habitat requirements of paddlefish as of 1986 are summarized in the Habitat Suitability Index models for paddlefish (Hubert et al. 1984; Crance 1987). Rosen (1976) reported that paddlefish prefer water depths of over 1.2 m for most of the year and 3 m or deeper during fall and winter. Cover is not considered a critical habitat component for paddlefish (Crance 1987). Rosen and Hales (1981) report that the optimal temperature range for paddlefish feeding is 7-20 degrees C and that temperatures in habitats inhabited by Polyodon ranged from near 0 to 28 degrees C. For juveniles, no specific information is available, but habitat use is suspected to be similar to that of adults; immature paddlefish have been reported to congregate with mature fish in tailwater areas during spring (Meyer 1960; Purkett 1963).

Little information is available concerning the minimal area in which paddlefish can live successfully. In the Upper Alabama River, Brantly (1987) determined that female paddlefish held larger linear home ranges than similarly-sized males throughout the year (36.3 vs 14.6 km in spring, 17.7 vs 6.3 km in summer, 14.3 vs 5.4 km in fall, and 16.6 vs 6.8 km during winter).

Studies by Meyer (1960), Gengerke (1978) and Southall (1982) are the main sources of life history and habitat use information on paddlefish in the UMR. Meyer (1960) investigated feeding and parasites of paddlefish. Gengerke (1978) obtained information on age, growth, and maturity. He also estimated exploitation rates and characterized the fishery. The impetus for the study was the legalization of recreational snag fisheries by Iowa in 1974 and by Illinois the year before (Ackerman 1975).

Southall (1982) radio-tagged a total of 17 paddlefish and investigated their habitat use during spring and summer. He also described the physical characteristics of their habitat. His fish averaged 81 cm in body length (BL; anterior edge of eye to fork of tail; Ruelle and Hudson 1977) with a range of 68 to 96 cm. Average estimated weight of the 17 fish was 8.3 kg (range: 4 to 18 kg). Of the 17 fish, seven were males, three were gravid females, and the other seven fish were of undetermined sex. Southall's study was conducted from June to August, 1980, and from March to August, 1981. During these periods, the average monthly discharges through Lock and Dam 13 were essentially normal: the mean monthly discharge averaged 11% below the long-term mean during June to August, 1980, and only 7% below normal for March to August, 1981. Unlike 1980, the gates of Lock and Dam 12 were fully opened during spring 1981, for a total of nine days; gates are typically opened for at least a few days each year (personal communication, Lorin Hager, U. S. Army Corps of Engineers, Rock Island District, Bellevue, Iowa). In contrast, during the drought period of 1988, the mean monthly discharges averaged only about one-half of the monthly means for March to August, and the gates were not opened.

Although seven habitat types have been identified in the UMR (tailwaters, main channel, main channel border, side channel, slough, and lake and pond; Rasmussen 1979), nearly three-fourths of Southall's (1982) telemetry contacts were made in only two of those types: tailwater (the deep and turbulent area immediately below the lock and dam), and main channel border habitat (areas near the main channel which had revetments, wing dams, sand bars, bridge supports or other features that created eddies or scour holes and reduced the current). The two habitat types had mean water depths of 14.8 and 6.7 m, and mean current velocities of 31.7 and 29.8 cm/s, respectively. However, several fish moved upstream out of the tailwaters during spring 1981, as soon as passage through the open gates was possible (Southall 1982; Southall and Hubert 1984).

Quiet backwater lakes were greatly under-utilized in proportion to the amount of available habitat. Paddlefish located in backwater lakes moved out of this habitat when the temperature approached 30 degrees C. In addition, no tagged paddlefish were located in the most lacustrine habitat above Lock and Dam 13. Backwater usage by paddlefish was restricted to those areas in the upper, more riverine, reach of the pool.

As part of a study recommended by Gengerke (1978) to identify spawning grounds of paddlefish, more than 30 large male and female paddlefish from Pool 13 were tagged with radio transmitters in 1988. These tagged fish provided an opportunity to assess movement and habitat use by larger fish than in Southall's study, as well as during a period of abnormally low river discharges. The objectives in this study were to investigate movement and habitat use by large paddlefish (most of which were gravid females) during the low-water conditions of 1988, and to compare these results with Southall's (1982) data on movements and habitat use from 1980 and 1981, which were from smaller fish during higher discharge conditions. Inasmuch as the habitat requirements of paddlefish seem to change as they grow (Coker 1930;

Thompson 1933), and as water conditions (e.g., discharges and river stages) vary between years (Southall 1982), information gained from this study would complement and clarify the significance of that previously collected.

STUDY AREA

General Information

The study was conducted below Lock and Dam 12 at Bellevue, Iowa (Figure 1; U. S. Army Corps of Engineers 1980). Lock and Dam 12 is one of 27 such structures located on the UMR, constructed in the 1930s by the United States Army Corps of Engineers to facilitate commercial navigation on the river.

Pool 12 lies above Lock and Dam 12 and extends northward 42.3 km to Dubuque, Iowa. Pool 13 begins at Lock and Dam 12 and ends 55 km downstream at Lock and Dam 13 at Clinton, Iowa. Peterson (1984) reviewed all scientific literature on the physical and biological resources of the UMR and also summarized the important recreational sites along the UMR. The ecology of Pools 11 to 13 of the UMR has been reviewed by Eckblad (1986).

Seven general habitat types in the UMR have been identified by the Upper Mississippi River Conservation Committee Fish Technical Section (Rasmussen 1979): tailwaters, main channel, main channel border, side channel, slough, and lake and pond. The main channel border can be further subdivided as either having or not having wing dams. These dams, constructed over the period 1873 through the

1930s, are impermeable channel training structures of stone and wood used to constrict river flow and stabilize the main channel (Schnick et al. 1982). Wing dams are typically submerged, but may provide a refuge from the current on the downstream side. In this study, sloughs, lakes, and ponds were classified together as backwaters. In terms of area, Pool 13 consists of 74.6% backwaters, 10.1% main channel, 5.3% main channel border without wing dams, 4.9% side channel, 4.8% main channel border with wing dams, and 0.3% tailwaters (Hurley 1983).

Water Conditions in Pool 13 in 1988

For two consecutive years (1987 and 1988), anomalously low precipitation and river discharges occurred throughout the midwestern United States, the UMR, and in Pool 13. From March to August, 1988, mean monthly flows through Lock and Dam 13 averaged 42% lower than the 47-year monthly mean (personal communication, Clint Beckert, U.S. Army Corps of Engineers, Rock Island, IL.). Mean monthly precipitation for this period at Dubuque, Iowa, also averaged 42% below the 125-year monthly means. During a typical spring season on the UMR, the gates of Lock and Dam 12 are opened for 10-15 days, permitting a free-flowing river (personal communication, Lorin Hager, U.S. Army Corps of Engineers, Rock Island District, Bellevue, Iowa). However, because of the abnormally low spring precipitation in the Upper Mississippi Valley in 1988, the gates of both Lock and Dam 12 and 13 were never fully opened.

In this study, physical data on river conditions in 1988 were separated into two distinct periods based on discharge. The first period (hereinafter called spring) began 11 March (Julian Day 71) and ended 20 May (Julian Day 141). Average daily discharge for this period was 1,530 cubic meters per second (range: 883 to 2,320). Average Lock and Dam 12 tailwater stage at 6 a.m. was 2.17 m (range: 1.64 to 2.83). Surface water temperature in the main channel was 13.8 C on 2 May and rose steadily to a maximum of 19.2 C near the end of this period. The second period (hereinafter called summer) began 21 May (Julian Day 142) and ended on 12 August (Julian Day 225). At Lock and Dam 12, discharge and tailwater stage were significantly lower ($p < 0.01$), and generally more stable during the summer period than during the spring period. Discharge during the summer period averaged 496 cubic meters per second (range: 346 to 1,269) and tailwater stage averaged 1.05 m (range: 0.88 to 1.92). Water temperature in the main channel increased during the period from 19.7 to 27.4 C (average 24.9 C; Figure 2). Lock and Dam 12 discharge and tailwater stage data were provided by the

U. S. Army Corps of Engineers, Rock Island District. Water temperatures in the main channel were monitored with a Peabody-Ryan Model J-90^{R} recording thermograph placed in the main channel about 0.5 km below Lock and Dam 12.

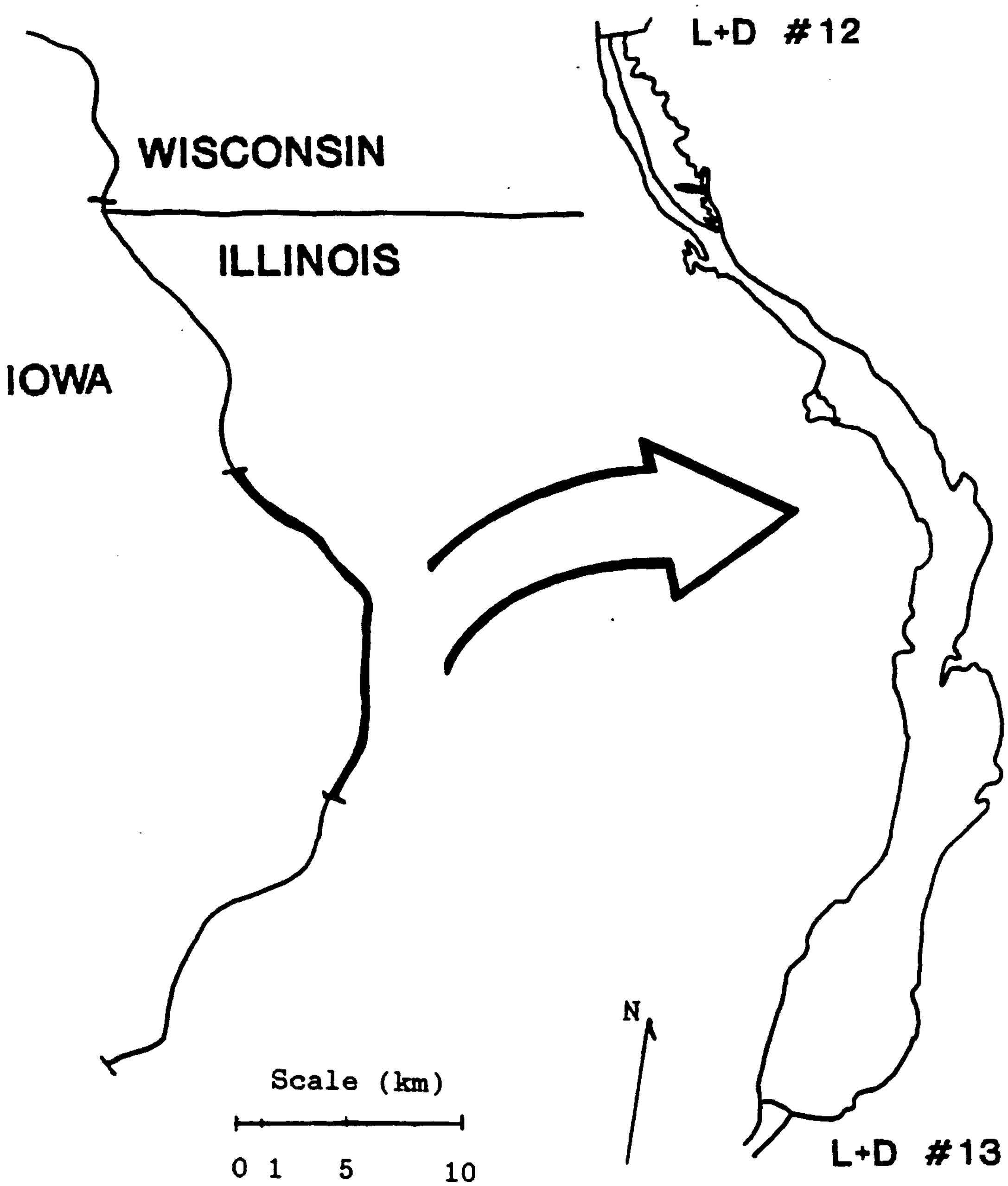
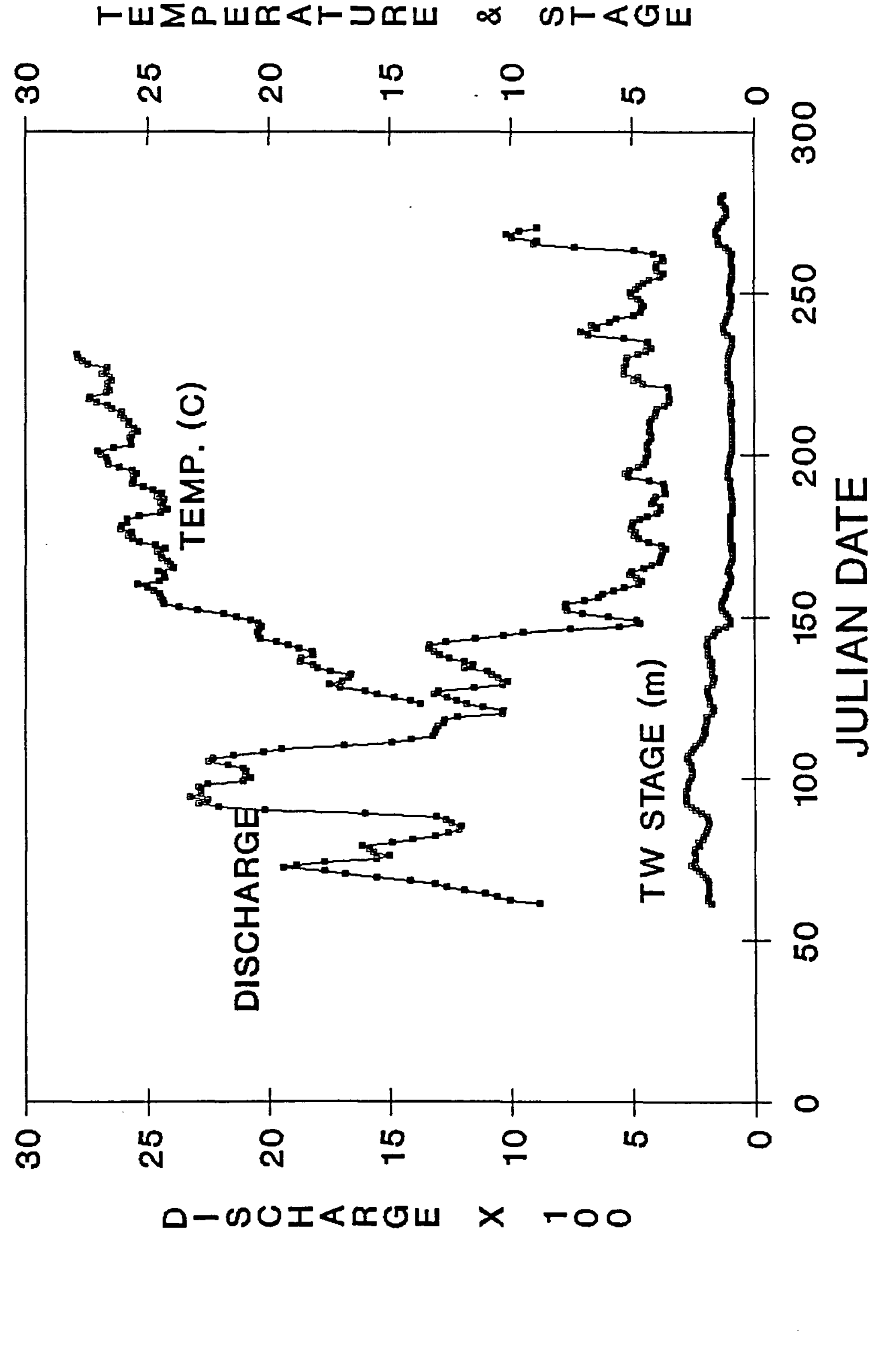


Figure 1. Study area, Pool 13, Upper Mississippi River

Figure 2. Lock and Dam 12 discharge (cubic meters per second), tailwater stage (m), and water temperature (C) in the main channel during spring and summer 1988 in Pool 13, Upper Mississippi River


DISCHARGE X 100
TEMPERATURE & STAGE
JULIAN DATE
DISCHARGE
TEMP. (C)
TW STAGE (m)
0
5
10
15
20
25
30
0
50
100
150
200
250
300

MATERIALS AND METHODS

Fish Capture

Thirty-five paddlefish were implanted with radio transmitters during the study (Table 1): 29 were collected by snagging between 11 and 17 March, 1988, and the other six fish were netted during summer. One of the six fish caught in summer was tagged with a radio transmitter that had not been previously implanted but the other five fish were tagged with radio transmitters recovered from fish that had been tagged earlier that spring and had died or lost their tags.

The snagging procedure involved rapidly jerking two large treble hooks vertically through the water until a fish was hit (Ackerman 1975; Anderson and Ackerman 1977; Beck 1978; Southall 1982). A typical snagging rig consisted of a heavy action sportfishing boat rod with roller-type line guides, 13-23 kg (30-50 lb)-test monofilament line, a heavy action reel, a large lead weight (to overcome strong tailwater currents and deep water) and the two large (No. 8/0) treble hooks, spaced about 1.5 m apart near the end of the line. Snagging was conducted from motor boats driven slowly and perpendicularly to the current in the tailwater area below Lock and Dam 12.

Table 1. Summary statistics for 35 paddlefish receiving surgically implanted radio transmitters in 1988 in Pool 13, Upper Mississippi River

Date Tagged	Freq.[a]	Sex	Condition	Total Length (cm)	Body Length (cm)	Girth (cm)	Weight (kg)
11 March	108	F	Mature	137	95	65	16.0
11 March	59	F	Mature	158	98	70	17.0
11 March	227	F	Mature	142	97	62	15.5
11 March	287[b]	F	Mature	[c]	114	76	25.4
11 March	168	F	Mature	133	96	71	17.7
13 March	86	F	Mature	148	105	74	22.2
14 March	179	F	Mature	136	100	65	17.5
15 March	408	F	Mature	145	105	71	21.0
15 March	248	F	Mature	145	96	64	15.5
16 March	328	F	Mature	152	107	70	19.3
17 March	188	F	Mature	150	103	69	18.8
17 March	20	F	Mature	153	105	74	22.0
3 June	148	F	Mature	152	110	70	21.3
3 June	367	F	Mature	153	106	64	19.0
1 July	349[b]	F	Mature	150	105	59	16.8
1 July	426	F	Mature	143	101	56	15.5
13 March	388	F	Maturing	[c]	101	63	17.1
13 March	298	F	Maturing	151	108	63	18.3
14 March	139	F	Maturing	143	94	62	14.6
15 March	158	F	Maturing	146	104	64	16.8
16 March	39	F	Maturing	147	100	66	18.2
16 March	257	F	Maturing	140	97	60	14.2
16 March	218	F	Maturing	143	101	68	18.0
16 March	419	F	Maturing	136	96	61	15.3
12 March	349	F	Immature	131	87	59	12.3
16 March	367	F	Immature	145	99	62	16.2
16 March	148	F	Immature	125	87	54	10.8
17 June	268[b]	F	Immature	122	79	47	7.3
11 March	116	M	Mature	128	87	58	12.5
12 March	78	M	Mature	131	88	48	10.3
16 March	239	M	Mature	126	83	53	9.6
17 March	128	M	Mature	123	87	49	9.2
1 July	59	M	Mature	132	88	49	9.7
12 March	376	M	Immature	130	90	58	11.8
16 March	426	M	Immature	111	75	45	6.3

[a] Frequency may be repeated if radio was reimplanted in a second fish.
[b] No movement or habitat use data obtained from this fish.
[c] Damaged or malformed rostrum.

The six fish collected during summer were captured in the tailwater area by towing 10.2 and 12.7 cm mesh gill nets from two boats headed in a downstream direction. The nets were towed through the middle of the water column. Captured fish were immediately removed from the net.

Telemetry Equipment

Thirty radio transmitters were obtained from Advanced Telemetry Systems, Isanti, Minnesota. The transmitters were manufactured to transmit in the range from 48.021 to 48.429 Mhz. Individual frequencies were separated by at least 0.009 Mhz. The lithium transmitter batteries had an expected life of 2.5+ years and delivered a transmission pulse every two seconds. The weight in air of a transmitter was 134 g (or 0.5 to 2.1% of a tagged fish's weight). Each transmitter was equipped with a 60 cm wire whip antenna. The radio receivers, also manufactured by Advanced Telemetry Systems, automatically scanned through the programmed series of radio frequencies while tracking. A large four-element Yagi antenna mounted in a 5.5 m flat-bottom boat with a 50 hp outboard motor completed the radio telemetry system.

Surgical Procedure

Radio transmitters were surgically implanted by using established techniques (Hart and Summerfelt 1975; Southall 1982; Brantly 1987). Each fish was positioned on the front deck of the boat and kept moist with a wet blanket. The fish tagged in summer were kept wet by submerging much of the fish in a large, water-filled trough. No anaesthetic was used. The incision site, the snag wound, and all surgical equipment were cleansed with Nolvasan^R antiseptic. The snag wound was always much less severe than the incision. A No. 11 scalpel blade was used to make an 8-10 cm incision into the body cavity about two-thirds down the side of the fish, above and anterior to the pelvic fins. A 15.2 cm director probe was used when making the incision to prevent damage to internal organs. Sexual condition was determined at this time by direct observation of the gonad through the incision. The transmitter was then inserted through the incision and positioned at the bottom of the body cavity; the wire whip antenna exited the body cavity about 6 cm posterior to the incision. The incision was closed with six to eight individual sutures using 3/8-circle cutting needles. One fish was sutured with 2-0 Prolene^R nylon suture material; all other fish were sutured with Braunimid^R 0 nylon. From each fish, data was collected on total length, body length, girth, and weight. Total processing time was between ten and 20 minutes per fish.

Fish were classified by the maturation state of the gonads. Three classes of females were defined: 1) ovaries with large, uniform dark eggs (mature); 2) ovaries with a mixture of smaller white and dark eggs, referred to as "salt and pepper" (maturing); and 3) ovaries with small white eggs (immature). Males were divided into two classes: 1) testes large and swollen (mature); and 2) testes small and flattened (immature). Of the 35 fish tagged, 16 were mature females, 8 were maturing females, 4 were immature females, 5 were mature males, and 2 were immature males (Table 1). Mature females ranged from 95 to 114 cm in body length (mean 103 cm) and 15.5 to 25.4 kg (mean 18.8 kg). Maturing females ranged from 94 to 108 cm in body length (mean 100 cm) and 14.2 to 18.3 kg (mean 16.6 kg). Immature females ranged from 79 to 99 cm in body length (mean 88 cm) and 7.3 to 12.3 kg (mean 11.7 kg). Mature males ranged from 83 to 88 cm in body length (mean 87 cm) and 9.2 to 12.5 kg (mean 10.3 kg) and the two immature males were 75 and 90 cm in body length and weighed 6.3 and 11.8 kg. Overall, the 35 paddlefish in this study averaged 97 cm in body length (range 75-114 cm) and 15.7 kg in weight (range 6.3-25.4 kg). These fish were almost twice the weight of the average fish studied by Southall in 1980 and 1981;

his fish ranged from 68 to 96 cm in body length (mean 81 cm) and four to 18 kg in weight (mean 8.3 kg).

Tracking Procedure

Radio-tagged paddlefish were searched for with the boat mounted antenna and receiver on a daily basis during daylight hours from 25 March to 12 August, 1988. Fish were also located on 1 and 2 October and 5 and 6 November, 1988, as well as periodically during the spring of 1989. Results presented here will emphasize data collected before 12 August, which is the most complete data available. Because of the large number of radio-tagged fish (30 paddlefish and 28 shovelnose sturgeon (*Scaphirynchus platorynchus*) for a concurrent project), a cycle of tracking through Pool 13 was usually initiated in the tailwater area because several fish were consistently in this habitat. This procedure greatly increased tracking efficiency because located fish could be deleted from the receiver's memory, thus allowing more rapid scanning for the remaining fish. A major effort was made to locate each fish once before the cycle of searching was begun again. When all fish were not located on a given day, search was resumed the following day at the last area scanned. Much of the study area was effectively searched from the main channel.

An airplane overflight was made on 11 August, 1988, to locate five fish which had not been found recently in the study area. A small loop antenna was attached to the airplane strut and wired to the scanning receiver. Pools 12 to 16 of the Upper Mississippi River were searched. The two missing fish contacted during the overflight were more accurately located by boat the next day.

When a fish was contacted during tracking, the location was plotted on U.S. Army Corps of Engineers maps (U. S. Army Corps of Engineers 1982) using visual triangulation of prominent terrestrial landmarks and the fish's proximity to in-river structures such as wing dams, islands or slough entrances identified on the maps. A fish was considered to be associated with a structure (e.g., a wing dam) when a contact was within approximately 200 m of the structure, based on maps and the observed current patterns at the site. At each contact, date, time, and habitat type (Rasmussen 1979) were recorded. Between 11 March and 12 August, 1988, the 32 fish that provided useable data were located a total of 774 times. The number of contacts per individual fish ranged from five to 39 (mean 24 and median 26).

Habitat Sampling

At 57 randomly-selected sites where radio-tagged paddlefish were located, the boat was anchored and six habitat variables were measured: surface water temperature (C), water depth, substrate type, and water velocity at three different depths (30 cm below surface, 0.6 x depth, and 30 cm above the substrate). Water depth was measured with a Humminbird LCR 200^R depth sounder. Velocity was measured to the nearest cm/sec with a Marsh-McBirney Model 201 Liquid Flow Meter^R. Substrate type was determined by visual inspection of samples collected with a Ponar dredge. Substrate was classified as mud, silt, fine sand, medium coarse sand, coarse sand, gravel with mussel shells, large rock, bedrock, or a combination of any two of the above types.

In addition to the above measurements, a transect perpendicular to the current was established at five randomly-selected paddlefish locations. Along each transect, the above six habitat measurements were taken at four stations and at the fish's location. All stations along a transect were equidistant from each other and from the banks. These transects provided a general profile of the river at a transect along the fish's location and provided information on whether the fish's location was keyed to a particular habitat variable.

Data Analysis

Data on fish movements and habitat use were analyzed with the aid of a Lotus 123 Worksheet (Lotus Development Corporation) and the Statistical Analysis System (SAS) (Helwig and Council 1979). Three fish were not included in any analysis because they either died or lost their transmitters shortly after implantation. A transmitter was considered to be stationary when two or three consecutive contacts were made at an identical site and if the signal could not be induced to change by noise made with the boat and outboard motor. In all analyses, the immature classes of both sexes were not considered separately because of small sample sizes. Immature males were combined with mature males to form a single class and immature females were combined with the maturing females. In all analyses, a p-value of less than 0.05 was necessary to reject a null hypothesis.

Movements were analyzed in six ways. First, each fish's pattern of upstream (positive) and downstream (negative) directional movements was examined for randomness with a nonparametric runs up-and-down test (Gibbons 1976). Secondly, an autocorrelation regression was calculated between the fish's latest movement and the preceding movement. These first two tests were made for each of the 27 fish that were located more than nine times.

Thirdly, the effect of changing discharge through Lock and Dam 12 (or a change in tailwater stage) on direction of movement was examined. Based on information from studies at other locations (Purkett 1963; Elser 1977; Pasch et al. 1978, 1980), it was hypothesized that paddlefish would move upstream with increasing discharge (or stage) and move downstream with decreasing discharge (or stage), perhaps especially so during spring. The mean movement of all fish located during a particular period of time was compared by regression methods with the change in Lock and Dam 12 discharge and the change in tailwater stage during that period. Analysis was performed for the two seasons, spring and summer, and for five groupings of fish: maturing females, mature females, all females, all males, and all fish.

Fourthly, the distances moved by individual fish between contacts were analyzed to investigate if differences existed in total movement between sexes and between seasons, and if there was any interactive effect of sex and season. Total movements were evaluated with an analysis of variance with the data set up in a split-plot design. This analysis was performed for the 15 fish (four males, six mature females and five maturing females) for which data were useable for the entire March to August period.

Fifthly, the range of the pool throughout which a fish was encountered was calculated to determine if any differences were evident between sexes or between mature and maturing females. A fish's range was calculated as the difference between the lowermost (downriver) and uppermost contacts. Ranges for the 15 fish in the previous analysis were calculated and compared with an analysis of variance.

Sixthly, rates of movement, expressed as straight-line distances between consecutive locations divided by the elapsed time between contacts, were compared between seasons, between sexes, and between mature and maturing females. Because this method of calculating movement rate can greatly underestimate the actual rate when consecutive contacts occur after a long time interval (Southall 1982), rates were calculated only for those contacts occurring within 48 hours of each other.

Habitat preferences of the radio-tagged paddlefish were evaluated with the use of Ivlev's electivity index (Ivlev 1961; Southall 1982). Electivity was defined as $E = (r_i - p_i)/ (r_i + p_i)$, where r_i is the percentage of telemetry contacts in a habitat type, and p_i is the percentage of that habitat type available in Pool 13. The index was used to indicate how fish used a particular habitat within Pool 13 in proportion to that habitat's abundance within the pool. Habitat use was also evaluated and compared with Habitat Suitability Index (HSI) data on paddlefish summarized by Hubert et al. (1984) and Crance (1987).

RESULTS

Movement

Pattern of movement

Only five of the 27 fish evaluated exhibited directional movements that significantly differed from random ($p < 0.05$). Each of these fish made a long series of downstream movements. Four of these five fish (Nos. 39, 108, 188, and 388) moved downstream into Pool 14: three in June or July and one (No. 108) in October. The fifth fish (No. 078) was located only nine times in a habitat other than the tailwaters, where it was effectively prevented from moving upstream.

For only three fish (Nos. 86, 179, and 248) was the succeeding movement negatively related to the previous movement ($p < 0.05$) and for no fish was the succeeding movement positively related to the previous movement ($p > 0.05$). Each of the three fish that displayed negatively autocorrelated movements made downstream (negative) movements of greater than ten kilometers followed by upstream movements of similar magnitude, or vice versa.

The movements of radio-tagged paddlefish varied greatly among individual fish; there was little indication of coordinated movements at the same time among fish. Tagged fish did not appear to move as groups, even during spring. The greatest directional movement by a study fish was made by maturing female No. 298, which moved downstream 92 km between May and August, 1988 (Figure 3). The greatest cumulative movement was made by mature female No. 248, which moved 435 km entirely within Pool 13 (Figure 4). Much of this movement was made during the low water conditions of summer.

The movements made by maturing female No. 139 were typical of those made by at least six of the paddlefish studied in 1988 (Figure 5). This fish was contacted almost exclusively in or near the tailwaters and was found to make relatively few movements out of this area. When the fish was not in the tailwaters of Lock and Dam 12, it was located near the wing dams across from the mouth of the Maquoketa River (approximate River Mile 548). Four males and at least two other females exhibited movements that were basically similar to this.

Another movement pattern common to a number of mature females was one of especially long movements during summer. This pattern was exemplified by mature female No. 20, which moved through Pool 13 from one dam to the other (Figure 6). The extreme example of this pattern is the movement of mature female No. 248, which moved between the dams a total of five times during summer (Figure 4). Similar movements were made

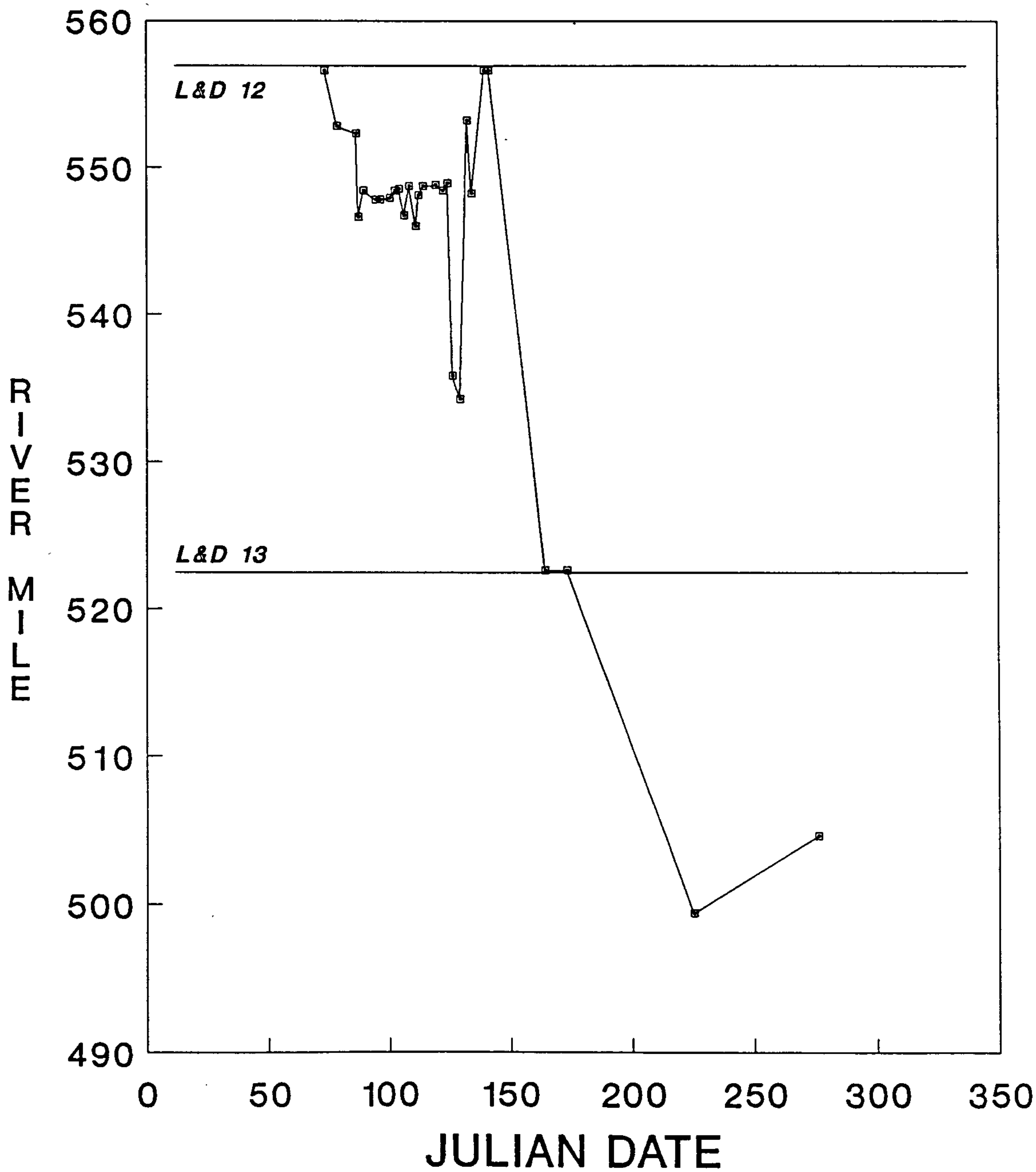


Figure 3. Movement by maturing female paddlefish No. 298 during 1988 in the Upper Mississippi River (28 contacts)

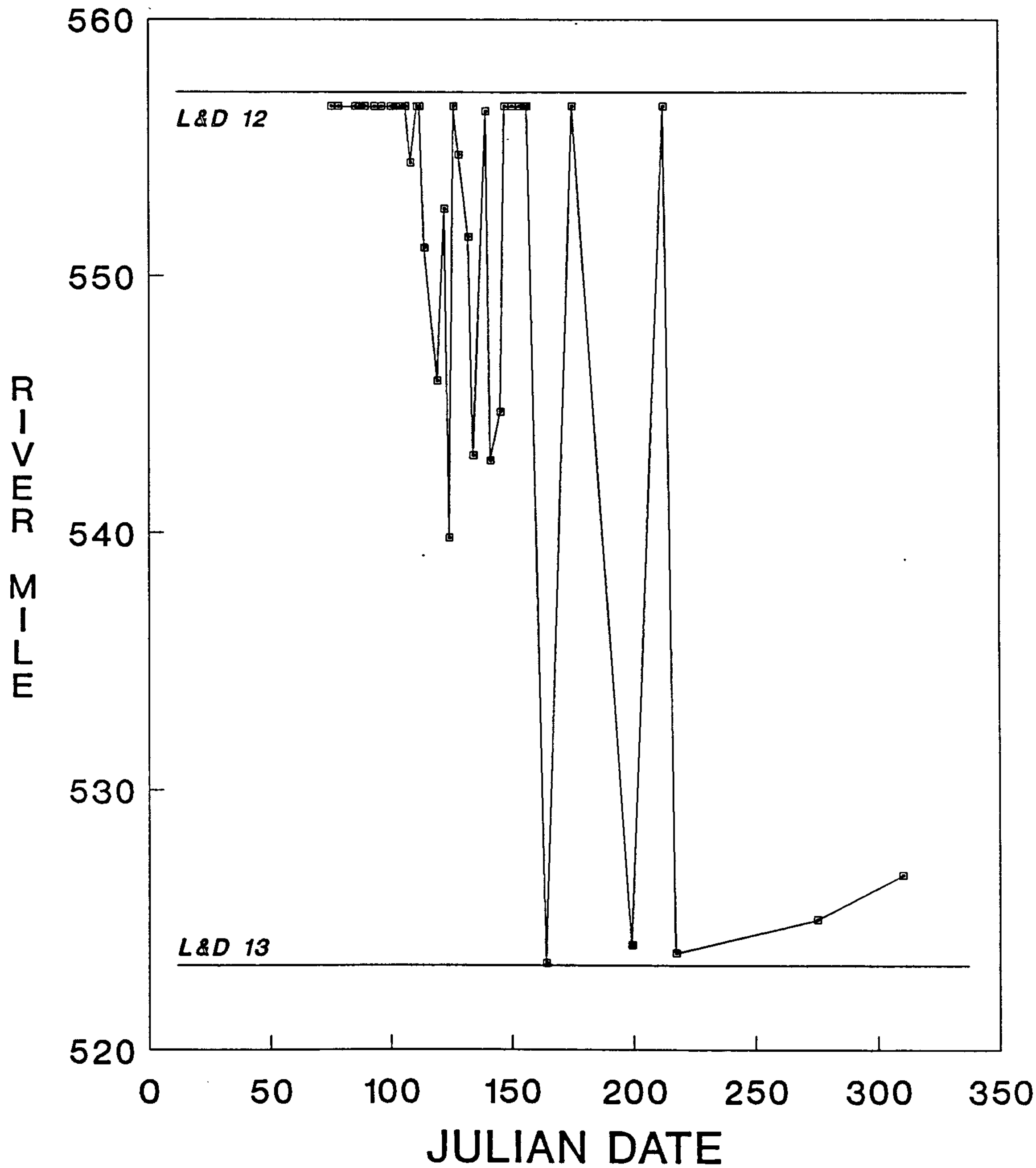


Figure 4. Movement by mature female paddlefish No. 248 during 1988 in the Upper Mississippi River (37 contacts)

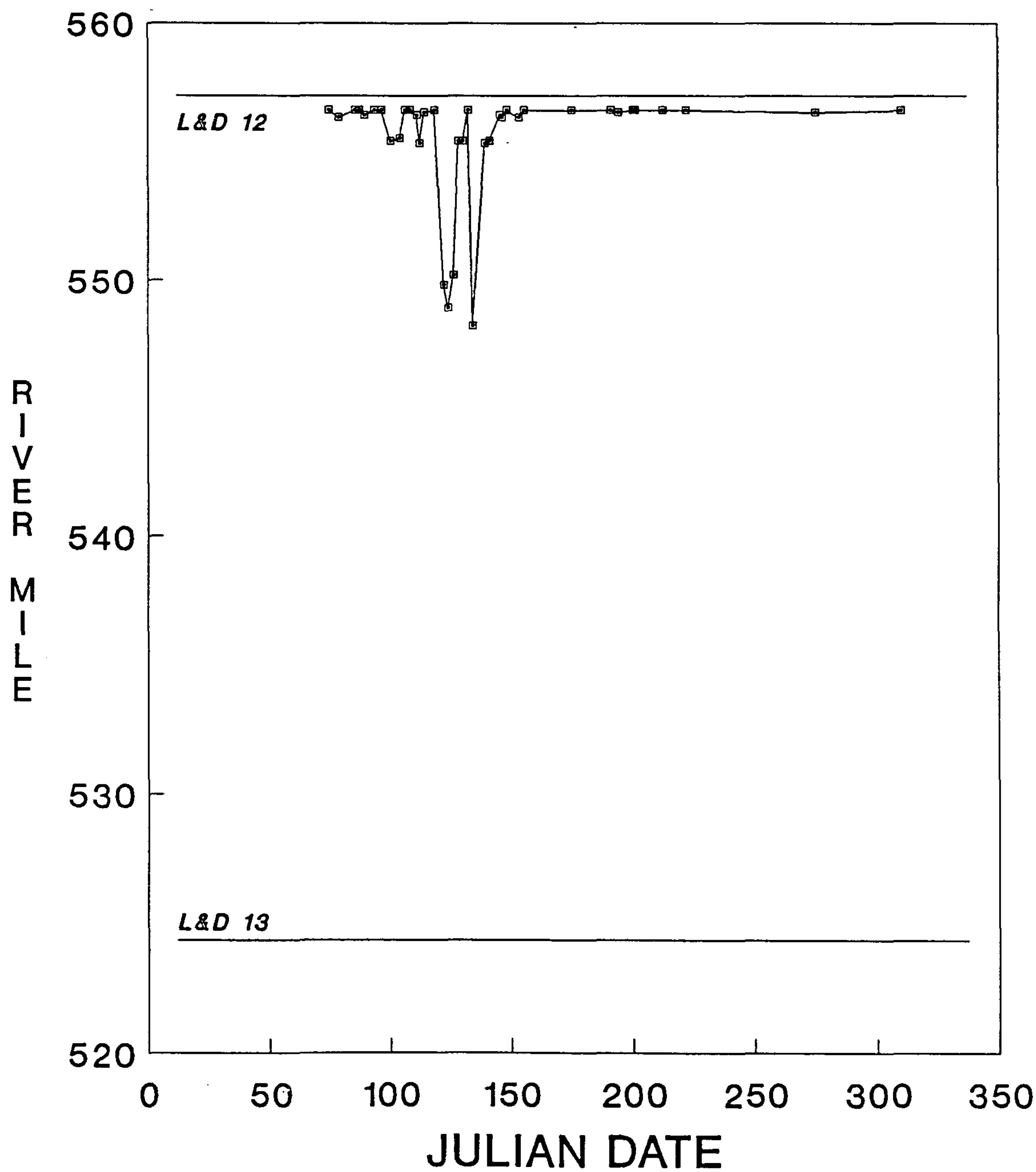


Figure 5. Movement by maturing female paddlefish No. 139 during 1988 in the Upper Mississippi River (38 contacts)

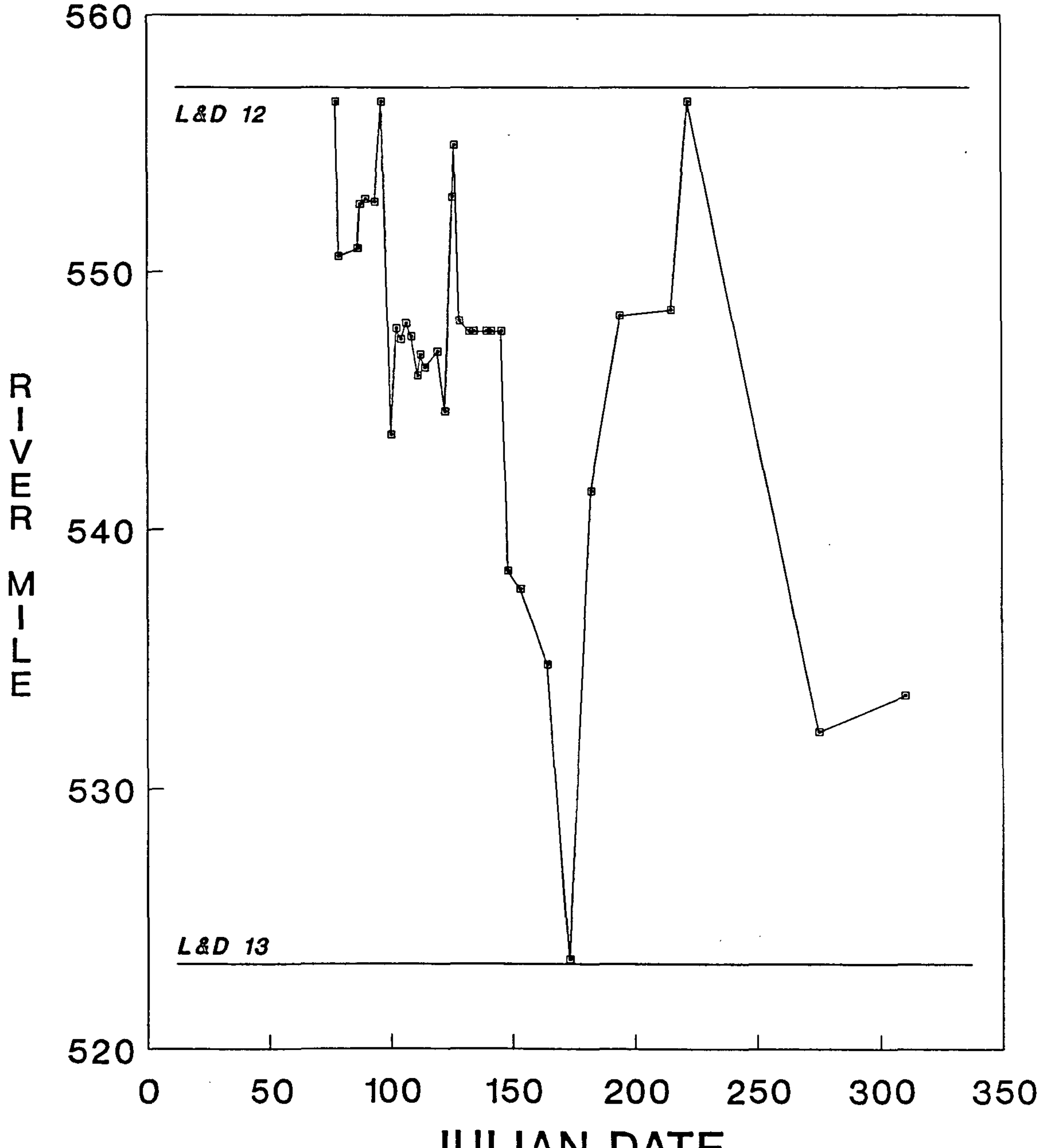


Figure 6. Movement by mature female paddlefish No. 20 during 1988 in the Upper Mississippi River (35 contacts)

by both mature and maturing females. However, these movements did not appear to be synchronized in time among individuals.

Movements of the other 28 radio-tagged paddlefish are presented in the Appendix.

Movement direction and river conditions

No relationship between Lock and Dam 12 discharge (or tailwater stage) and mean direction of fish movement was observed for any group of fish during either spring or summer. For each season, sex, and maturation state, the slope of the regression line was indistinguishable from zero (F-test; $p > 0.05$) and the correlation coefficient low ($\leq$ 0.51; degrees of freedom 1,4 to 1,36). Thus, in 1988, it was not clear that paddlefish moved upstream as discharge and stage increased.

Three-fourths of all contacts with radio-tagged paddlefish in 1988 were made during spring (the potential spawning period), yet no evidence was found of congregation or synchronized migration.

Distance moved between observations

No significant difference was found in distance moved between observations between sexes or between seasons for the

15 fish evaluated ($p > 0.05$). During spring, four males moved an average of 1.9 km per observation, six mature females 4.2 km, and five maturing females 2.5 km. During summer, the males moved an average of 3.6 km per observation, mature females 9.3 km, and maturing females 4.6 km. Mean movement per observation for all 15 fish was 3.0 km during spring and 6.2 km during summer. Paddlefish may have actually been more mobile during summer than spring, or this result may have resulted from fewer observations during summer (191 observations versus 583 during spring). Over the period from March to August (spring and summer combined), males moved an average of 2.5 km per observation, mature females 5.8 km, and maturing females 2.9 km; these differences also were not significant ($p > 0.05$). In addition, the interaction between sex and season was not significant ($p > 0.05$). The high variation in movements between individual fish made it difficult to detect any significant differences in these analyses. However, female paddlefish, which were larger than the males, appeared to be more mobile.

Linear ranges

The distance between the lowermost and uppermost telemetry contacts with a fish was significantly different between males (mean 19 km; range 13 to 25) and females (mean 39 km; range 14 to 60; $p < 0.05$). The ranges of mature females (mean 46 km; range 36 to 54) and maturing females (mean 31 km; range 14 to 60) were not significantly different ($p > 0.05$). The number of contacts (on which the range for each fish was based) was similar for each of the 15 fish (range 27 to 37 contacts; mean 33; standard deviation 3.3).

Movement rates

Mean movement rates, calculated for periods of less than 48 hours, were not significantly different ($p > 0.73$) between spring (mean 86 m/hr) and summer (mean 97 m/hr), nor were any significant differences observed between males (mean 77 m/hr) and females (mean 92 m/hr; $p > 0.57$). Maturing females did not exhibit significantly different rates (mean 94 m/hour) than mature females (mean 89 m/hour; $p > 0.84$). In addition, the same analyses using $\log_{10}$-transformed rates did not indicate any significant differences. Comparisons of movement rates between seasons for males and for the two maturation stages of females were not performed because of insufficient numbers of encounters by group during summer.

Habitat Use

Of the 774 times that radio-tagged paddlefish were contacted between 11 March and 12 August, 1988, 304 encounters (39%) occurred in the tailwaters, 260 (34%) in the main channel border with wing dams, and 128 (16%) in the main channel border without wing dams (Figure 7 and Table 2). Few encounters with radio-tagged paddlefish were made in the other habitat types: main channel 8%, backwaters 2% and side channels less than 1%. Because the most commonly used habitats are scarce in Pool 13, three-fourths of all encounters occurred in about 5% of the available habitat (Figure 7), whereas the most abundant habitat type, the backwaters, had only 2% of the contacts.

The distribution of encounters among the habitat types did not differ greatly between spring (583 encounters) and summer (191 encounters; Table 2). Paddlefish were most commonly located in the tailwaters: 37% of all encounters during spring and 48% of the encounters during summer were made there. Encounters in the main channel border with wing dams constituted 34% of all contacts in spring and 33% in summer. Number of contacts in the main channel border without wing dams decreased from 20% in spring to 7% in summer. Use of backwaters remained low in both seasons. Ten different radio-tagged paddlefish were located a total of 14 times in the most lacustrine backwater area immediately above Lock and Dam 13. Use of the main channel remained constant (8% in spring, 7% in summer), as did use of side channels (<1% in spring, 1% in summer).

During spring, frequency of use of the tailwaters and main channel borders with and without wing dams differed only slightly among the three fish groups (males, mature females, and maturing females; Figure 8). Males and maturing females were encountered slightly more frequently in the tailwaters than mature females (41% and 38% versus 32%). Use of the main channel border with wing dams was essentially the same for all three groups (males, 33% of all spring encounters; mature females, 34%; and maturing females, 34%), as was use of the main channel border without wing dams (males 17%, mature females 23%, and maturing females 19%). Use of the main channel was limited for all fish (10% of the contacts with mature females, 8% for maturing females and 6% for males), as was use of backwaters (4% by males, 1% by mature females, and <1% by maturing females). Use of side channels was essentially nil during spring (<1% for each group).

During summer, both male and female paddlefish were strongly associated with the tailwaters -- and males even moreso than females. Sixty-five percent of the contacts with males, 41% of the contacts with mature females and 40% of the

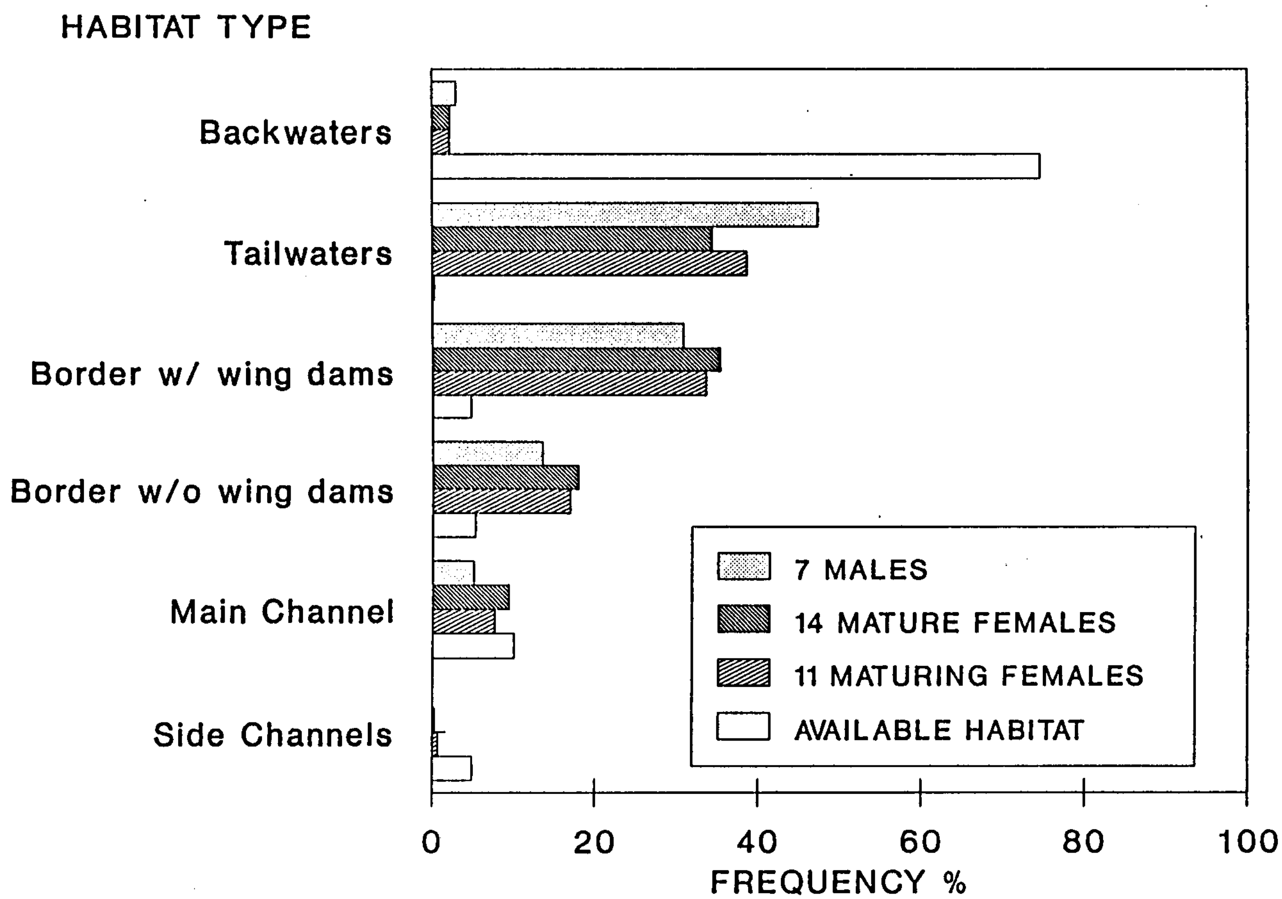


Figure 7. Frequency of use of habitat types by paddlefish during spring and summer (11 March to 12 August) 1988 in Pool 13, Upper Mississippi River (Border refers to main channel border)

Table 2. Number of paddlefish of each sex category and the number of contacts (and %) in each habitat type for spring (Sp) and summer (Su) 1988 in Pool 13, Upper Mississippi River

	Males		Mature Females		Maturing Females		Total	
	Sp	Su	Sp	Su	Sp	Su	Sp	Su
Number of Fish	6	6	11	11	11	9	28	26
HABITAT TYPE								
Tailwaters	58 (41)	36 (65)	72 (32)	33 (41)	83 (38)	22 (40)	213 (37)	91 (48)
Main Channel Border with Wing Dams	47 (33)	14 (25)	76 (34)	32 (40)	74 (34)	17 (31)	197 (34)	63 (33)
Main Channel Border without Wing Dams	24 (17)	3 (5)	51 (23)	4 (5)	40 (19)	6 (11)	115 (20)	13 (7)
Main Channel	8 (6)	2 (4)	22 (10)	7 (9)	17 (8)	4 (7)	47 (8)	13 (7)
Backwaters	6 (4)	0 (0)	2 (1)	5 (6)	1 (<1)	5 (9)	9 (2)	10 (5)
Side Channels	0 (0)	0 (0)	1 (<1)	0 (0)	1 (<1)	1 (2)	2 (<1)	1 (1)
Total	143	55	224	81	216	55	583	191

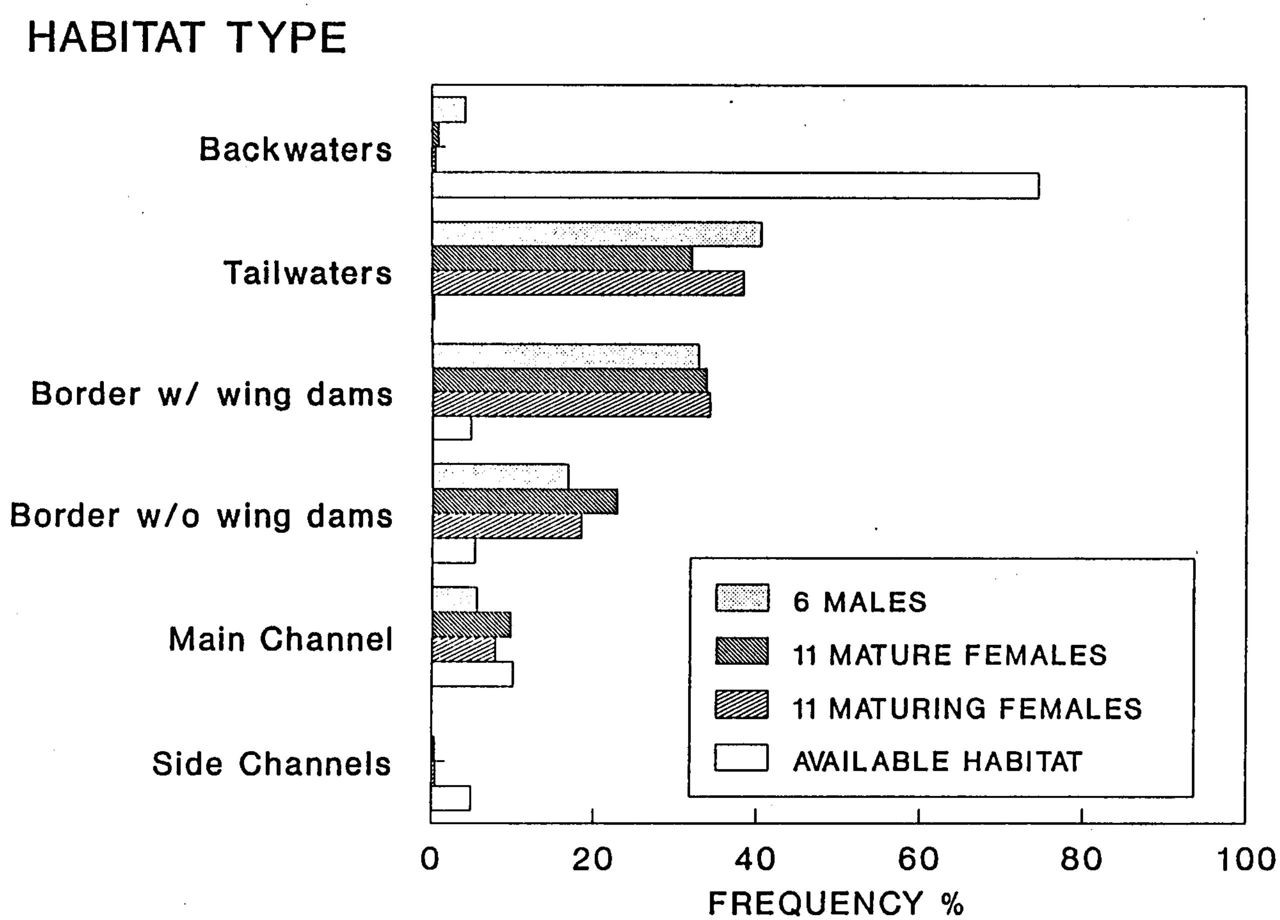


Figure 8. Frequency of use of habitat types by paddlefish during spring (11 March to 20 May) 1988 in Pool 13, Upper Mississippi River (Border refers to main channel border)

contacts with maturing females were made there (Figure 9). As in spring, the main channel border with wing dams had the next highest number of contacts. And also as in spring, use of the main channel was low: 4% of the contacts with males, 9% of the contacts with mature females, and 7% of the contacts with maturing females were made in this habitat. No males or mature females were contacted in side channels, and only 2% of the contacts with maturing females were in this habitat. No males were located in backwaters during summer, and only 6% of the encounters with mature females and 9% of those for maturing females were in backwaters.

Only two habitats were utilized in proportion to availability: the main channel (by mature females during spring) and the main channel border without wing dams (by mature females during summer; Figures 8 and 9). Therefore, paddlefish were preferentially selecting habitat in the river. Ivlev's electivity index (Ivlev 1961; Southall 1982), which was used to measure this selection, indicated that paddlefish strongly selected for the tailwaters and for main channel borders with wing dams. Electivity by all fish for the tailwaters and for the main channel border with wing dams averaged 0.99 and 0.74, respectively, over spring and summer combined (Figure 10). Males, mature females, and maturing females displayed similar selection for these two habitats during both spring and summer (Figures 11 and 12). Selection for main channel borders without wing dams by all groups was moderate (average E value = 0.57) during spring, but decreased to near zero for males and mature females during summer. Selection by maturing females for this habitat remained higher largely because of one fish's (No. 257) preference for a specific reach of the pool.

Avoidance of the main channel was weak ($-0.16 \leq$ E value ≤ 0) for females and was more pronounced for males (E value in summer = -0.47). Inasmuch as females appeared to move more than males, they were more likely to use the main channel when moving the longer distances. During both seasons, backwaters and side channels were avoided by paddlefish (average E values of -0.91 and -0.85, respectively).

Distribution of paddlefish locations in Pool 13

More than two-thirds (69%) of the paddlefish contacts were made in four specific areas in Pool 13 (Figure 13). The first area was the upper kilometer of the pool, including the tailwaters, which had 46% of all contacts. When paddlefish were not located within the tailwaters, they were frequently associated with one of th*e three wing dams adjacent to it. The second area included the four wing dams across from the

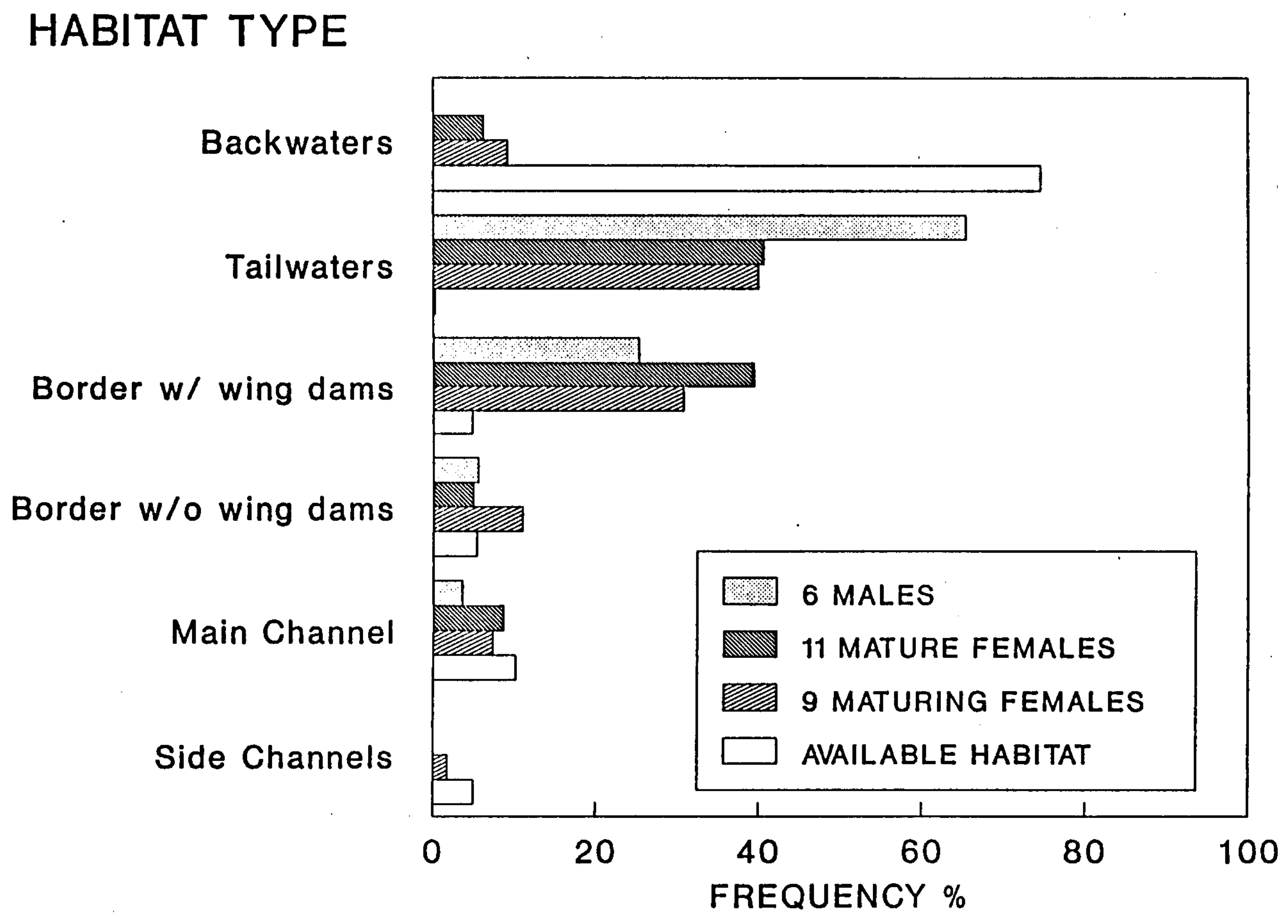


Figure 9. Frequency of use of habitat types by paddlefish during summer (21 May to 12 August) 1988 in Pool 13, Upper Mississippi River (Border refers to main channel border)

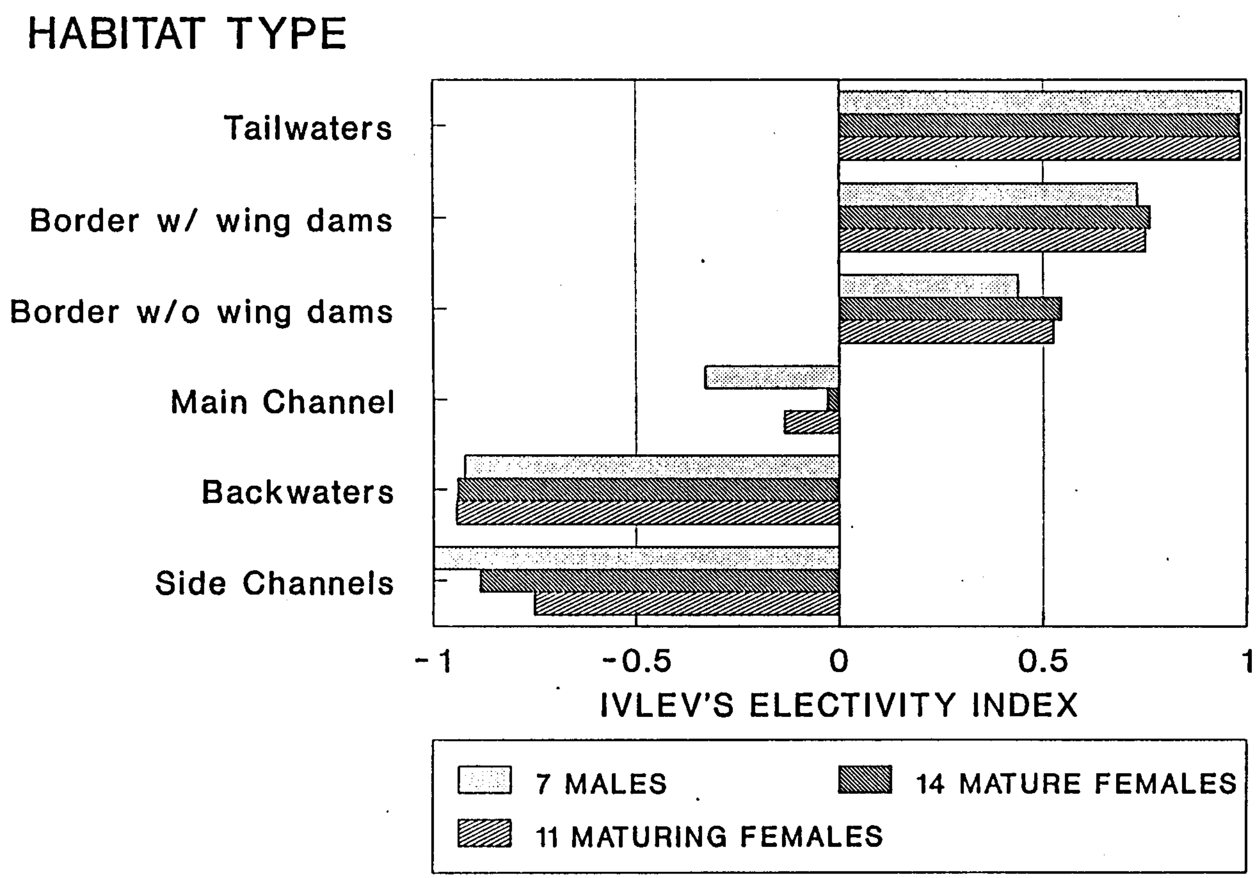


Figure 10. Ivlev's electivity values for habitat preference by paddlefish during spring and summer (11 May to 12 August) 1988 in Pool 13, Upper Mississippi River (Border refers to main channel border)

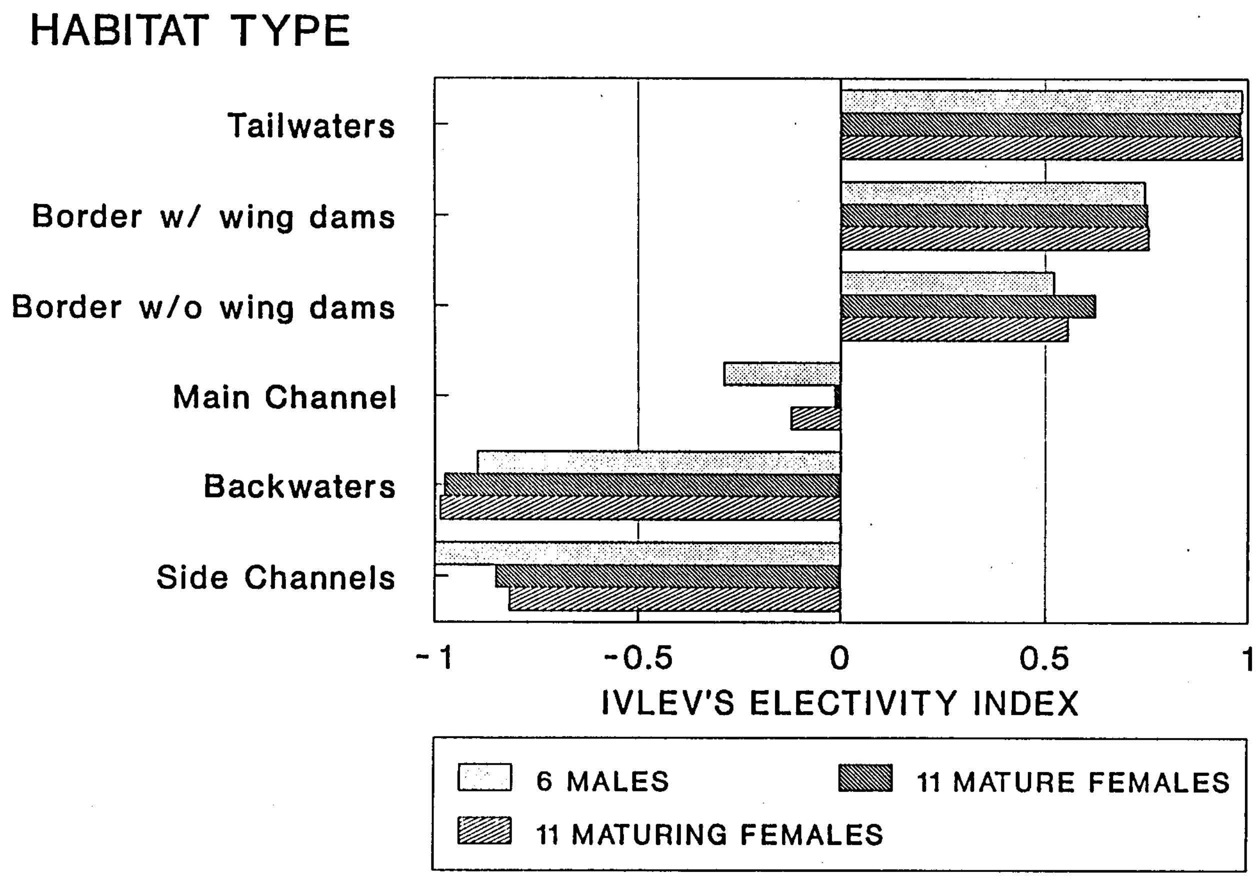


Figure 11. Ivlev's electivity values for habitat preference by paddlefish during spring (11 March to 20 May) 1988 in Pool 13, Upper Mississippi River (Border refers to main channel border)

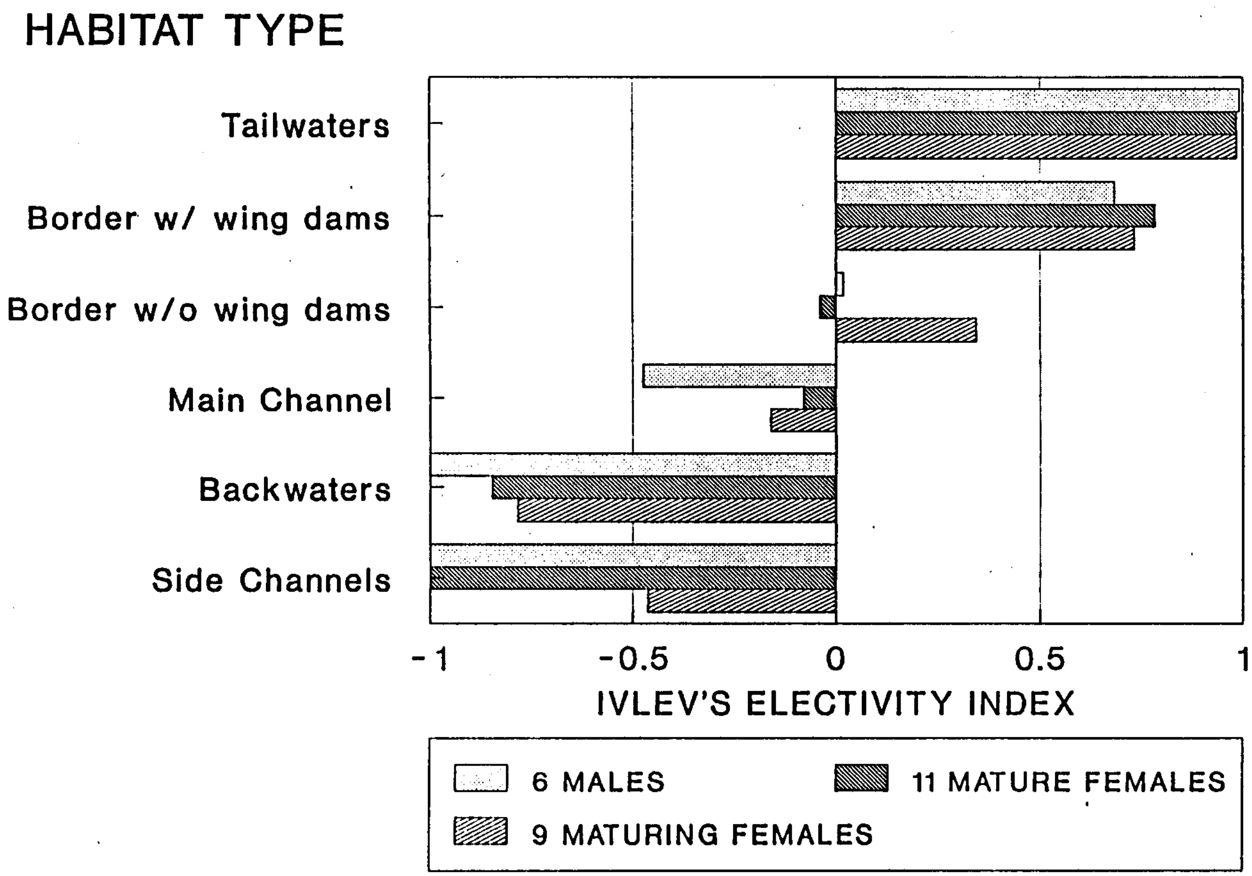


Figure 12. Ivlev's electivity values for habitat preference by paddlefish during summer (21 May to 12 August) 1988 in Pool 13, Upper Mississippi River (Border refers to main channel border)

mouth of Crooked Slough (River Mile 550), and accounted for 6% of all contacts. Only 13% of all encounters with paddlefish were made in the eight kilometers between these two areas (and 1% in Crooked Slough). The third area, which included the series of nine wing dams across and downstream from the mouth of the Maquoketa River (River Mile 548), had 11% of all contacts. Only 4% of all contacts were made between areas two and three. The fourth important area, located much further downstream, was the series of three wing dams across from Sabula, Iowa (River Mile 534.5). This area accounted for 6% of all encounters. Only 10% of all encounters were made in the 19 kilometers between areas three and four; the lowest 18 kilometers of Pool 13 below the fourth area accounted for only 3% of the contacts. In 1988, paddlefish were obviously preferring these four areas.

Physical description of habitat at locations of radio-tagged paddlefish

Mean water depth, substrate type, surface temperature, and current velocity at three depths for 57 summer paddlefish locations are presented in Tables 3 and 4. A total of 36 paddlefish were located in the tailwaters when the 11 tailwater samples were taken; otherwise, each habitat sample described a single fish's location. Mean depth was greatest in the tailwaters (15.7 m), where current velocities were also generally the greatest and the most variable (range 0.02 to 0.89 cm/s). Depth of the backwater locations (mean = 5.9 m) is not characteristic of this habitat because two samples were taken from an unusually deep hole (greater than 9 m) about 100 m upstream of Lock and Dam 13. Substrate type at most locations was a combination of sand and silt, which appeared to be dominant throughout the pool. Temperature varied only slightly between habitat types.

In comparing the habitat characteristics at five stations along the transects, none of the habitat variables differed substantially between the fish location and the other stations on the transect (Table 5). These results did not suggest that paddlefish were particularly attracted to a specific level of a measured habitat variable (depth, current velocity, substrate type or temperature).

Spring 1989 Telemetry Results

Between 31 March and 10 April, 1989, the gates of Lock and Dam 12 were taken out of operation, which allowed the river to flow freely. Although the open gates provided the paddlefish with access to Pool 12, radio-tagged paddlefish which were monitored on 1-2 April, 15-16 April, and during summer 1989 had not moved upstream (except perhaps for short movements that were not monitored). This result suggested continued preference by paddlefish for the tailwater habitat.

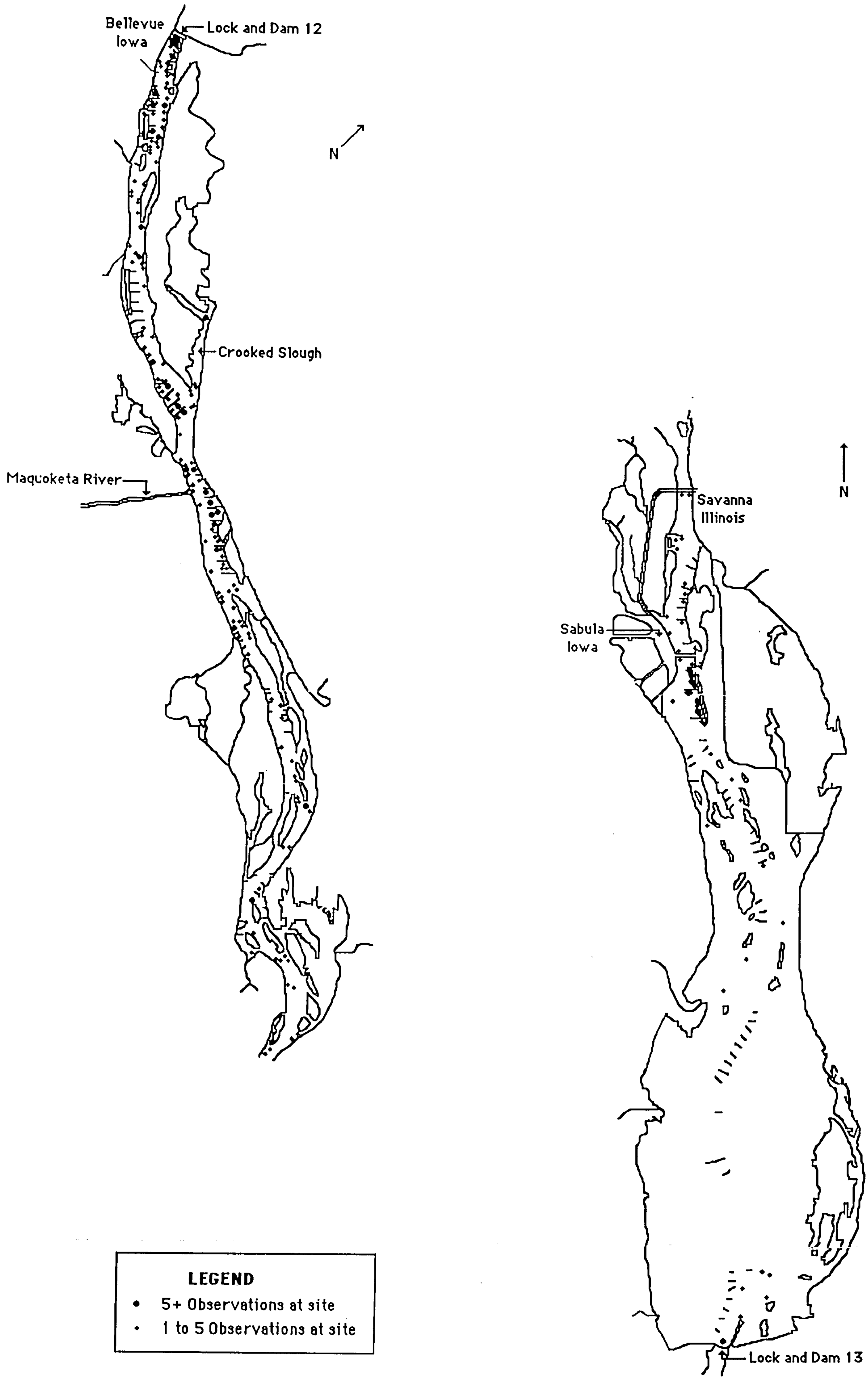


Figure 13. Distribution of 774 radio-tagged paddlefish encounters during March to August 1988 in Pool 13 of the Upper Mississippi River

Table 3. Means (and standard deviations) of selected habitat characteristics at paddlefish locations within a habitat type, summer 1988 in Pool 13, Upper Mississippi River

			Current Velocity (m/s)		
Habitat type	(n)	Depth (m)	Surface	0.6x depth	Bottom
Tailwaters	11	15.7(4.6)	0.29(0.21)	0.24(0.10)	0.11(0.06)
Channel border with wing dams	32	5.2(1.4)	0.18(0.09)	0.14(0.09)	0.09(0.07)
Channel border w/o wing dams	5	5.5(2.4)	0.22(0.03)	0.22(0.07)	0.16(0.07)
Main channel	4	6.1(0.9)	0.19(0.08)	0.17(0.07)	0.16(0.05)
Backwater lakes	5	5.9(3.5)	0.05(0.05)	0.10(0.09)	0.04(0.04)
Side channels	0				

Table 4. Substrate type and mean (and standard deviation) surface temperature found at paddlefish locations by habitat type, summer 1988 in Pool 13, Upper Mississippi River

Habitat type	Surface Temperature (C)	Most frequent substrate type (No. encountered/total No. substrates sampled)
Tailwaters	24.7(2.6)	medium coarse sand and silt, and/or bedrock (9/11)
Channel border with wing dams	24.3(2.8)	medium coarse sand and silt (11/31); fine sand and silt (6/31)
Channel border w/o wing dams	26.5(1.0)	sand and silt (3/5); gravel and dead mussels (2/5)
Main channel	25.2(1.9)	sand, silt, dead vegetation (3/4)
Backwater lakes	27.3(2.0)	silt, dead vegetation, sand (4/5)

Table 5. Habitat characteristics at five paddlefish locations and at four other locations along each of the five transects, summer 1988 in Pool 13, Upper Mississippi River

	Depth (m)	Temperature (C)	Current (m/s) Top	0.6x	Bottom
Fish locations (n=5)					
Mean	4.09	28.1	0.162	0.132	0.090
Standard Deviation	2.07	0.7	0.097	0.079	0.056
Four other stations along transect (n=20)					
Mean	4.51	28.4	0.135	0.121	0.090
Standard Deviation	1.83	1.0	0.112	0.092	0.077

DISCUSSION

Mortalities and Lost Transmitters

Overall, more than half of the fish tagged in 1988 suffered mortality or tag loss within a year. The cause of mortality for several radio-tagged paddlefish was identified. Commercial fishermen of Pools 13 and 14 caught and killed five fish (four in 1988 and one in 1989). Four fish were caught and killed in the recreational snag fishery below Lock and Dam 12 in winter 1988, and spring 1989, and two others were caught, landed, and successfully released in January, 1989. In all, 11 of 35 (31%) radio-tagged paddlefish were captured by fishermen within a year after release.

The most reliable estimates of total annual exploitation of paddlefish in Pool 13 (Gengerke 1978) were obtained over the four-year period from 1975 to 1978 from returns of tags by anglers. Mortality rates ranged from 2% for fish less than 90 cm in length to 10% for fish greater than 90 cm in length. The mean mortality rate for all fish combined over the four years was 6%. Five of the 17 (29%) paddlefish radio-tagged by Southall (1982) in 1980 were caught by fishermen within two years: four were caught commercially and one was snagged. Thus, in 1988, the known harvest rate of radio-tagged paddlefish within one year after tagging was about twice as high as for Southall's (1982) fish and about five times the average annual exploitation rate originally estimated by Gengerke (1978). However, because of the small sample size of paddlefish in 1988, the extremely low river levels, and the unusually mild weather in January, 1989, the estimated rates from 1988 may be higher than typical exploitation rates in the late 1980s. Under the prevailing low water conditions, paddlefish may have been concentrated more than usual. In addition, during the mild weather in January, 1989, the tailwater area was generally free of ice, and snagging success may have been abnormally high (personal communication, John Pitlo, Iowa Department of Natural Resources, Bellevue, Iowa). Under these conditions, it is likely that the observed exploitation rate was correspondingly high. With more typical water levels and winter ice conditions, exploitation rates might be similar to that reported by Gengerke (1978).

During summer 1988, one dead paddlefish that had never been radio-tagged was recovered in the main channel and another was recovered in the main channel border. One of these fish had been snagged, tagged with two Floy tags in its rostrum, and released in March, 1988, when transmitters had been implanted in other fish. This fish had evidently received numerous severe cuts and had been buried by a recreational boater. The second large paddlefish had several long wounds which were still bleeding, and its caudal fin was freshly severed at the caudal peduncle. These two fish had probably died from these large wounds, which were most likely caused by collisions with boats. Similar accidents may have caused the death of some of the radio-tagged paddlefish. This potential cause of mortality has also been recognized by Meyer (1960), who collected numerous scarred paddlefish in Pool 13, and by Southall (1982), who recovered several mutilated, dead paddlefish in the same pool. In the Missouri River, 36% of the paddlefish examined had scars as a result of collisions with boats or snagging and several fish had died because of injuries received from the collisions (Rosen and Hales 1980). These incidents will probably increase in the future as recreational and commercial use of the river increases.

Twelve additional radio-tagged paddlefish either died of unknown causes or lost their transmitters at some point during the period from 11 March to 25 July, 1988. Three dead fish were recovered in backwater areas in the lower half of Pool 13 between May and July, 1988, but were too decomposed for the cause of death to be determined. Three transmitters remained stationary in the river shortly after implantation in fish, and the six other transmitters became stationary after longer periods of time (from 33 to 92 days after implantation). For none of these 12 fish is it known if the fish died, lost its transmitter through the incision, or expelled its transmitter during spawning.

One cause of mortality may have been related to the surgical procedure. All fish did not recover equally well from transmitter implantation. Two radio-tagged fish snagged in early 1989 had not healed properly from surgery. One fish had a large, infected wound at the incision site and the other fish had lost the transmitter, presumably through the incision site. However, two other radio-tagged fish that were snagged and released had healed well and showed no inflammation or irritation around the incision site. A third radio-tagged fish, which was snagged but later killed, had also healed well. Winter (1983) noted that incisions may heal slowly in cold water. Inasmuch as most of the paddlefish used in this study were tagged in March, when water temperatures were below 5 C, several fish may have healed slowly, developed infections around the incision sites, and suffered mortality or tag loss as a result. More study is needed to determine the best time of the year to tag paddlefish so that healing is enhanced.

Movements

Although radio-tagged paddlefish exhibited substantial movements during the drought conditions of 1988, no fish moved upstream through Lock and Dam 12 during 1988 or when the gates were fully opened during April, 1989. Six fish did, however, move downstream into Pool 14 between June and November, 1988. Five of these fish were contacted at least once immediately above Lock and Dam 13 prior to entering Pool 14. In addition, the most active fish (No. 248) was also located on one occasion immediately above the dam. These results indicated that the dams probably prevented upstream movement between pools and impeded downstream movement between pools.

Results of the present study, however, indicate that paddlefish can evidently pass downstream through partially closed dam gates without sustaining major injuries. Coker (1929) and Southall (1982) had also suggested that such movement was feasible. But the only course for an upstream-bound paddlefish, other than through an open gate, is through a navigation lock. Although Gengerke (1978) suggested that paddlefish may use the locks to move between pools of the UMR, no radio-tagged paddlefish in this study were found directly below, above or inside a navigation lock. Some upstream movement might conceivably occur when gates are temporarily open for repair or maintenance (Southall 1982). An individual gate was occasionally opened for repair or maintenance in 1988. However, before the gate was lifted, a bulkhead was installed both upstream and downstream of the gate and the water pumped out before the gate was actually opened (personal communication, Clint Beckert, U. S. Army Corps of Engineers, Rock Island, Illinois). It seems unlikely that paddlefish could move through such an operation.

Despite the lack of upstream movement when the gates were opened for 11 days in spring 1989, results of this study strongly suggested that interpool movements of paddlefish are impeded by the gates being closed and by the absence of fish passage facilities on locks and dams. At any time during the study, several paddlefish were located immediately below Lock and Dam 12. One fish in particular (No. 248; Figure 4) exhibited repeated upstream and downstream movements between Locks and Dams 12 and 13 that were characteristic of a caged organism. Dams have also been reported to prevent upstream movements of paddlefish in the Upper Mississippi River (Coker 1929; Southall and Hubert 1984), the Missouri River (Rehwinkel 1978; Rosen et al. 1982; Unkenholz 1982), and the Osage River (Russell et al. 1980). The longest paddlefish movements documented have occurred in open, undammed river systems or stretches (Russell 1986), such as in the lower Missouri River, where a paddlefish moved more than 1900 km in about two years (from Gavins Point Dam on the Missouri River to Smithland Dam on the Ohio River; Unkenholz 1982).

Only one in five of the paddlefish radio-tagged in 1988 exhibited a pattern of movement which was identified as non-random. About one in five (5 of 27) of the fish displayed a long series of consecutive downstream movements and four of these fish moved into Pool 14. (Two other fish moved into Pool 14 in 1988 but did not display this clustered pattern of movements). Evidence suggests that there may have been nonrandom movements during short intervals of the study period (Figure 6, Appendix Figures A19 and A23). However, when examined over the entire period, these short sequences were not significant.

Several paddlefish exhibited homing abilities. Three fish demonstrated negatively autocorrelated directional movements resulting from alternating upstream and downstream movements. Other researchers have reported that paddlefish make occasional, directed excursions from a familiar range and quickly return (Southall 1982; Brantly 1987). Such directed excursions may have been exhibited by additional fish in the study but were not revealed by telemetry.

Direction of movement was not related to changes in either flow through Lock and Dam 12 or tailwater stage for any of the sex groups (males, maturing females, mature females, all females, and all fish) during either spring or summer. This result contrasts markedly with results from several other studies. Purkett (1963), Elser (1977), and Pasch et al. (1978, 1980) have all reported that paddlefish moved upstream with increasing water level or discharge, especially during spring. These studies were able to relate markedly increased recreational or commercial harvests of paddlefish in tailwater areas to substantial rises in river levels. In the Upper Alabama River system, Brantly (1987) recently documented strong upstream response by female paddlefish to increasing discharge and temperature during spring and fall, whereas males were not noticeably affected during spring, summer or fall. In the present study, certain movements by individual fish followed the expected pattern of upstream movement, but other fish moved downstream under the same conditions, making detection of the relationship difficult. Perhaps the low 1988 river conditions and the lack of a sufficient spring flood did not induce major, synchronized upstream movements. Graham et al. (1975) and Southall (1982) also found it difficult to determine any relationship between river conditions and direction of movement for all periods of changing river stage.

Although movement rates were not significantly different between males and females, male paddlefish exhibited significantly smaller linear ranges than females during March to August, 1988, and tended to remain near the tailwaters of Lock and Dam 12. Southall (1982) did not compare ranges between sexes, but in the Upper Alabama River, Brantly (1987) also reported that ranges were larger throughout the year for female paddlefish than for males of a similar size.

The maximum movement rate exhibited by a paddlefish in 1988 was 1.3 km/hr over a 26-hour period. This rate is within the range of common swimming speeds (of about 1.6 km/hr) reported for paddlefish (Graham et al. 1975). Southall (1982) found that his smaller radio-tagged paddlefish moved within Pool 13 at rates of up to 5.1 km/hr for 2.4 hours. During 1988, the larger paddlefish did not exhibit such high swimming rates over the elapsed times of 17 to 48 hours encountered in this study. The difference in time elapsed between contacts may explain this apparent difference in movement rates.

Habitat Use

Habitat use in 1988 by the large paddlefish, most of which were females, showed both similarities and differences when compared with Southall's (1982) smaller fish. Paddlefish in both studies showed strong preferential selection for the tailwaters and the main channel border with wing dams during both spring and summer. However, the frequency of use of the tailwaters by paddlefish in 1988 was twice the frequency found in 1980 and 1981 (Southall 1982). Four of every ten encounters with radio-tagged paddlefish in 1988 were in the tailwaters below Lock and Dam 12. The scour holes and eddies associated with tailwater areas are evidently even more important to large paddlefish than to smaller ones.

As in Southall's (1982) study, about one-half of all contacts were made in the main channel border. In 1988, paddlefish were contacted twice as often in the main channel border with wing dams as in the main channel borders that did not have wing dams. In both the present study and in Southall's (1982) study, results indicate that the protection from current and the creation of eddies provided by wing dams (or similar natural structures such as sand bars) creates areas well-suited to paddlefish (Rosen et al. 1982; Southall 1982).

Overall, more than two-thirds of all encounters with radio-tagged paddlefish were made in four small areas of Pool 13. These areas, which constituted less than 10% of the area of the pool, had several characteristics which paddlefish may have preferred. Each area, including the heavily-used tailwaters below Lock and Dam 12, had a series of at least three wing dams. As Southall (1982) noted, man-made structures such as wing dams and the lock and dam reduce the current substantially from that in the main channel and also create eddies. In addition, a scour hole more than six meters deep had formed behind at least one wing dam in each area, and the average depth in the tailwaters was 15.7 m. During spring, paddlefish may have been searching these wing dam or tailwater areas for possible spawning sites since the closed gates prevented upstream movement. These areas may provide the rocky substrate and current characteristics which Purkett (1961) reported were necessary for paddlefish reproduction.

The four areas also probably provided good feeding opportunities because each area was located immediately downriver of an entrance to a backwater area. The importance of backwaters as food producing areas for fishes such as the paddlefish has been noted by many researchers, including Kofoid (1903), Stockard (1907), Wagner (1908), Alexander (1915), Rosen (1976), Rosen et al. (1982), Southall (1982), Southall and Hubert (1984), Sheaffer (1984), and Eckblad (1986). Paddlefish in the UMR feed primarily on immature aquatic insects (Hoopes 1960; Meyer 1960). Eckblad et al. (1984) and Sheaffer (1984) found that substantial numbers of macroinvertebrates, including aquatic insects, drift out of backwater areas such as Crooked Slough toward the main channel. Densities of macroinvertebrates transported from backwater habitats were higher in the main channel border downstream from the mouth of the backwater than in areas upstream of the confluence (Sheaffer 1984). For the wing dams below Crooked Slough, densities of benthic macroinvertebrates were higher in the rocky substrate of the wing dams than in the main channel and other main channel border areas where the substrate was primarily sand (Hall 1980; Pierce 1980; Corley 1982). With these conditions, the four areas probably provided paddlefish with prime feeding opportunities.

The turbulent nature of the currents in the tailwaters, and perhaps in these deep scour holes, may allow paddlefish to swim slowly yet remain almost stationary (unless disturbed) while feeding on drifting invertebrates. The depths of these areas may offer some form of protection or cover that is difficult to define at present. Other areas in the pool with wing dams, such as the area between Sabula, Iowa, and Savanna, Illinois (four wing dams), or the area above the outlet of Crooked Slough on the Iowa side (seven wing dams; Figure 13), did not have deep scour holes nor slow and variable currents, and were not located near an entrance to a backwater. These areas were only occasionally used by paddlefish.

Paddlefish occasionally used the lake-like habitat above Lock and Dam 13 in 1988, but did not use this area at all during Southall's (1982) study. The reasons for this difference are not known. Conversely, only five fish were contacted (a total of nine out of 774 times, or about 1% of the contacts) in the backwaters of Crooked Slough during spring and summer 1988, whereas Southall (1982) made about 80 of 518 contacts (15%) with paddlefish in these backwaters. It is also not known why the backwaters of Crooked Slough were used so much less frequently in 1988 than in 1980 and 1981, but three possible explanations are offered.

First, perhaps the habitat use reflected the location of capture. All fish tagged in 1988 were captured in the tailwaters immediately below Lock and Dam 12, whereas most fish in Southall's (1982) study were captured at the mouth of Crooked Slough, about 11 river kilometers downstream from the tailwaters. It is possible that fishes snagged in the tailwaters would be less likely to enter Crooked Slough than would fish netted near Crooked Slough. However, because 13 fish snagged in the tailwaters were later found near the mouth of Crooked Slough (fish Nos. 20, 39, 78, 86, 139, 179, 188, 218, 257, 328, 388, 419, and 426), and paddlefish were highly mobile in the pool, this explanation is the most unlikely of the three.

A second possible explanation is that because the fish studied in 1988 averaged 7.4 kg larger than those studied by Southall (1982), their habitat preference may be different than the smaller fish. This explanation also is unlikely because three of the five fish found in Crooked Slough in 1988 were among the larger fish tagged.

A third possible explanation is that the low water levels during 1987 and 1988 may have made certain backwaters in Pool 13 either too shallow, too vegetated, or too warm for paddlefish during summer and perhaps limited them to areas nearer the main channel. Field observations in Crooked Slough indicated that some areas were less than one meter deep during summer and this depth is considered unsuitable for paddlefish (Crance 1987). Growths of filamentous algae may have also been a factor. Southall (1982) found that paddlefish moved out of Crooked Slough when water temperature approached 30 C in 1980, and, although water temperatures were not measured in Crooked Slough in 1988, high water temperatures are commonly associated with drought years. In Pool 13, Sheaffer (1984) found water temperatures in backwaters to be significantly higher than in the main channel ($p < 0.10$). All three of the above explanations may have contributed to the observed reduction in backwater use in 1988 compared to 1980 and 1981.

Comparison with Habitat Suitability Index Models

The habitat characteristics at sites where paddlefish were encountered were, with a few exceptions, in general agreement with the two present Habitat Suitability Index (HSI) models for adult paddlefish (Hubert et al. 1984; Crance 1987). Paddlefish were encountered at locations which generally had depth and velocity characteristics within the ranges considered to be acceptable or optimal for the species (Index values of 0.5 to 1; Hubert et al. 1984; Crance 1987). Ninety-one percent of the locations sampled had depths of three meters or greater, the optimal range according to Hubert et al. (1984). However, 67% were over five meters deep, which is the greatest depth plotted on the SI curve of Hubert et al. (1984). In addition, 30% of these locations had depths over seven meters, the upper limit to the optimal range of Crance (1987). Large paddlefish of Pool 13 were evidently using areas which had greater depths than the models indicated. Because the depth at which the paddlefish were located in the water column in these deep areas is not known, it is not clear how frequently the paddlefish are actually using the deep water and how frequently they are merely located over the deep water. Observations of the snag fishery, however, provided circumstantial evidence that many adult paddlefish are located near the bottom throughout the winter. It is also true that some of the best paddlefish snagging occurs below Lock and Dam 12 (Anderson and Ackerman 1977; Carlson and Bonislawsky 1981), which has a deeper scour hole (about 24 m) below it than do most of the surrounding pools (personal communication, Tom Boland, Iowa Department of Natural Resources, Bellevue, Iowa). The great depths may thus provide valuable habitat for paddlefish.

Current velocities at paddlefish locations generally supported the HSI models. Eighteen percent of the locations in 1988 had mean current velocities less than 0.07 m/s, the optimal range, and 95% had velocities less than 0.30 m/s which is within the acceptable range of the HSI models (Hubert et al. 1984; Crance 1987). Mean current velocity at the paddlefish locations was 0.16 m/s (standard deviation 0.09; range 0.01 to 0.50).

Temperature at the locations was typically higher than optimal according to the HSI models (Hubert et al. 1984). Only four percent of the contacts were made where temperatures were within the optimal range of 7 to 20 C (Hubert et al. 1984) and 37% of the contacts were made where temperatures were within the optimal range reported by Crance (1987) of 13 to 24 C. Although water temperature was not routinely measured at locations where paddlefish were contacted, temperatures near 30 C were recorded in the main channel and in backwater areas, indicating that paddlefish were perhaps using the coolest water available during the warm and dry weather of 1988.

RECOMMENDATIONS FOR MANAGEMENT AND FUTURE RESEARCH

Although the number of fish tagged in this study was rather large for a radio-telemetry study, it was not sufficient to permit the estimation of population size or exploitation. A tagging and creel survey should be conducted to determine whether exploitation rates may have changed in the past 12 years since Gengerke's (1978) estimates were made. Recent technological advances, such as improved depth sounders, may have increased snagging success.

Movements and habitat use of adult paddlefish in the UMR during various river levels have been investigated in this study and by Southall (1982). These studies and Meyer's (1960) were performed, in part, to locate paddlefish spawning and rearing areas. However, this objective remains to be accomplished. In addition, little information is available concerning juvenile paddlefish (those weighing less than about five kilograms). Studies on these topics would assist paddlefish management in the Upper Mississippi River.

ACKNOWLEDGMENTS

This project was the result of efforts by many people from several organizations, including the Department of Animal Ecology at Iowa State University, the Iowa Cooperative Fish and Wildlife Research Unit, and the Iowa Department of Natural Resources. Financial support was provided by the Iowa Department of Natural Resources. I wish to sincerely thank the following people for their valuable input and assistance: Dr. Dennis Scarnecchia, Dr. John Ramsey, John Pitlo, Maurice Anderson, Dennis Weiss, Tom Boland and Tom McCarthy. Special appreciation is offered to Gary Curtis for his daily field assistance. Dr. Paul Hinz provided helpful assistance with data analysis. Clint Beckert and John Schliekalman of the U.S. Army Corps of Engineers, Rock Island, Illinois, provided water discharge and stage data for Pool 13. Wayne and Rita Kress permitted use of their dock for collection of water temperature data. I would like to thank my parents and brothers for their varied forms of support throughout this project. Finally, Troy Jacobsen, Gary Siegwarth and Mike Stueck assisted with the snagging of paddlefish in the inclement weather that is March in Iowa.

LITERATURE CITED

Ackerman, G. L. 1975. Iowa's first snagging season for paddlefish. Iowa Conservationist 34(2):6-9.

Alexander, M. L. 1915. More about paddlefish. Transactions of the American Fisheries Society 45:34-39.

Anderson, M., and G. L. Ackerman. 1977. Fire in the hole. Iowa Conservationist 36(2):8-9.

Beck, D. 1978. The ponderous paddlefish. Iowa Conservationist 37(3):2-3.

Brantly, T. B. 1987. Paddlefish movements in the Upper Alabama River. Master of Science Thesis. Auburn University, Auburn, Alabama.

Burr, B. M. 1980. Polyodon spathula (Walbaum), paddlefish. Pages 45-46 in D. S. Lee, C. R. Gilbert, C. H. Hocutt, R. E. Jenkins, D. E. McAllister, and J. R. Stauffer, Jr., editors. Atlas of North American Freshwater Fishes. North Carolina State Museum of Natural History, Raleigh.

Carlson, D. M., and P. S. Bonislawsky. 1981. The paddlefish (Polyodon spathula) fisheries of the midwestern United States. Fisheries (Bethesda) 6(2):17-22, 26-27.

Carlson, D. M., M. K. Kettler, S. E. Fisher, and G. S. Whitt. 1982. Low genetic variability in paddlefish populations. Copeia 1982(3):721-725.

Coker, R. E. 1929. Keokuk Dam and the fisheries of the Upper Mississippi River. Bulletin of the United States Bureau of Fisheries 45:87-139.

Coker, R. E. 1930. Studies of common fishes of the Mississippi River to Keokuk. Bulletin of the United States Bureau of Fisheries 45:141-225.

Corley, S. D. 1982. Influence of wing dam notching on fish, aquatic macroinvertebrates, hydrographic relief, current velocity, substrate, water temperature, and dissolved oxygen in Pool 13, Upper Mississippi River. Master of Science Thesis. University of Wisconsin, Stevens Point.

Crance, J. H. 1987. Habitat suitability index curves for paddlefish, developed by the Delphi technique. North American Journal of Fisheries Management 7:123-130.

Eckblad, J. W. 1986. The ecology of Pools 11-13 of the Upper Mississippi River: a community profile. United States Fish and Wildlife Service Biological Report 85(7.8).

Eckblad, J. W., C. S. Volden, and L. S. Weilgart. 1984. Allochthonous drift from backwaters to the main channel of the Mississippi River. American Midland Naturalist 111:16-22.

Eddy, S., and P. H. Simer. 1929. Notes on the food of the paddlefish and the plankton of its habitat. Transactions of the Illinois State Academy of Science 21:59-68.

Elser, A. A. 1977. Paddlefish investigations. Montana Department of Fish and Game. Dingell-Johnson Project F-30-R-13, Job Number 2-A, Progress Report.

Evermann, B. W. 1902. Description of a new species of shad (Alosa ohiensis) with notes on other food fishes of the Ohio River. Report of the United States Commission on Fish and Fisheries 1901:273-288.

Fitz, R. B. 1966. Unusual food of a paddlefish (Polyodon spathula) in Tennessee. Copeia 1966(2):356.

Gengerke, T. W. 1978. Paddlefish investigations. Iowa Conservation Commission. United States National Marine Fisheries Service Project 2-225-R, Segment 1-3, Final Report.

Gengerke, T. W. 1986. Distribution and abundance of paddlefish in the United States. Pages 22-35 in J. G. Dillard, L. K. Graham, and T. R. Russell, editors. The paddlefish: status, management and propagation. American Fisheries Society, North Central Division, Special Publication 7, Bethesda, Maryland.

Gibbons, J. D. 1976. Nonparametric methods for quantitative analysis. Holt, Rinehart and Winston, New York.

Graham, L. K., T. R. Russell and E. J. Hamilton. 1975. Maintenance of the Osage River paddlefish fishery: Quarterly report to U. S. Army Corps of Engineers, Kansas City District. Missouri Department of Conservation, Columbia.

Hall, T. J. 1980. Influence of wing dam notching on aquatic macroinvertebrates in Pool 13, Upper Mississippi River: the prenotching study. Master of Science Thesis. University of Wisconsin, Stevens Point.

Harlan, J. R., and E. B. Speaker. 1956. Iowa fish and fishing. Iowa Conservation Commission, Des Moines.

Hart, L. G., and R. C. Summerfelt. 1975. Surgical procedures for implanting ultrasonic transmitters into flathead catfish. Transactions of the American Fisheries Society 104(1):56-59.

Helwig, J. T., and K. A. Council. 1979. SAS users guide. SAS Institute, Raleigh, North Carolina.

Hoopes, D. T. 1960. Utilization of mayflies and caddis flies by some Mississippi River fishes. Transactions of the American Fisheries Society 89(1):32-34.

Houser, A., and M. G. Bross. 1959. Observations of the growth and reproduction of the paddlefish. Transactions of the American Fisheries Society 88(1):50-52.

Hubert, W. A., S. H. Anderson, P. D. Southall, and J. H. Crance. 1984. Habitat suitability index models and instream flow suitability curves: paddlefish. United States Fish and Wildlife Service Biological Services Program FWS/OBS-82/10.80.

Hurley, S. T. 1983. Habitat associations and movements of shovelnose sturgeon in Pool 13 of the Upper Mississippi River. Master of Science Thesis. Iowa State University, Ames.

Ivlev, V. S. 1961. Experimental ecology of the feeding of fishes. Yale University Press, New Haven, Connecticut.

Kofoid, A. A. 1903. Plankton studies. IV. The plankton of the Illinois River, 1894-1899, with introductory notes upon the hydrography of the Illinois River and its basin. Part I. Bulletin of the Illinois State Laboratory of Natural History 6 (1901-1903):95-629.

Lagler, K. F., J. E. Bardach, R. R. Miller, and D. M. Passino. 1977. Ichthyology. Second Edition. John Wiley and Sons, New York.

MacAlpin, A. 1947. Paleopsephurus wilsoni, a new polyodontid fish from upper Cretaceous of Montana, with a discussion of allied fish, living and fossil. Contributions from the Museum of Paleontology, University of Michigan 6(8):167-234.

Meyer, F. P. 1960. Life history of Marsipometra hastata and the biology of its host Polyodon spathula. Doctoral Dissertation. Iowa State University, Ames.

Nichols, J. T. 1916. A large Polyodon from Iowa. Copeia 1916(34):65.

Pasch, R. W., and C. M. Alexander. 1986. Effects of commercial fishing on paddlefish populations. Pages 46-53 in J. G. Dillard, L. K. Graham, and T. R. Russell, editors. The paddlefish: status, management and propagation. American Fisheries Society, North Central Division, Special Publication 7, Bethesda, Maryland.

Pasch, R. W., P. A. Hackney, and J. A. Holbrook. 1978. Ecology of the paddlefish, Polyodon spathula (Walbaum), in Old Hickory Reservoir, Tennessee, with emphasis on first year life history and the effects of impingement at Gallatin Steam Plant on the population. Tennessee Valley Authority, Division of Water Resources, Development Report, Knoxville.

Pasch, R. W., P. A. Hackney, and J. A. Holbrook. 1980. Ecology of paddlefish in Old Hickory Reservoir, Tennessee, with emphasis on first-year life history. Transactions of the American Fisheries Society 109(2):157-167.

Peterson, G. A. 1984. Resources inventory for the Upper Mississippi River (Guttenberg, Iowa to Saverton, Missouri). United States Fish and Wildlife Service, Rock Island, Illinois.

Pflieger, W. L. 1975. The fishes of Missouri. Missouri Department of Conservation, Jefferson City.

Pierce, R. B. 1980. Upper Mississippi River wing dam notching: the pre-notching fish study. Master of Science Thesis. University of Wisconsin, Stevens Point.

Purkett, C. A., Jr. 1961. Reproduction and early development of the paddlefish. Transactions of the American Fisheries Society 90(2):125-129.

Purkett, C. A., Jr. 1963. The paddlefish fishery of the Osage River and the Lake of the Ozarks, Missouri. Transactions of the American Fisheries Society 92(3):239-244.

Rasmussen, J. L. 1979. A compendium of fishery information on the Upper Mississippi River. Upper Mississippi River Conservation Committee, Rock Island, Illinois.

Rehwinkel, B. J. 1978. The fishery for paddlefish at Intake, Montana during 1973 and 1974. Transactions of the American Fisheries Society 107(2):263-268.

Rosen, R. A. 1976. Distribution, age and growth, and feeding ecology of paddlefish (*Polyodon spathula*) in unaltered Missouri River, South Dakota. Master of Science Thesis. South Dakota State University, Brookings.

Rosen, R. A., and D. C. Hales. 1981. Feeding of paddlefish, *Polyodon spathula*. Copeia 1981(2):441-455.

Rosen, R. A., D. C. Hales, and D. G. Unkenholz. 1982. Biology and exploitation of paddlefish in the Missouri River below Gavins Point Dam. Transactions of the American Fisheries Society 111(2):216-222.

Ruelle, R., and P. L. Hudson. 1977. Paddlefish (*Polyodon spathula*): growth and food of young of the year and a suggested technique for measuring length. Transactions of the American Fisheries Society 106(6):609-613.

Russell, T. R. 1986. Biology and life history of the paddlefish--a review. Pages 2-20 *in* J. G. Dillard, L. K. Graham, and T. R. Russell, editors. The paddlefish: status, management and propagation. American Fisheries Society, North Central Division, Special Publication 7, Bethesda, Maryland.

Russell, T. R., L. K. Graham, D. M. Carlson, and E. J. Hamilton. 1980. Maintenance of the Osage River - Lake of the Ozarks paddlefish fishery. Missouri Department of Conservation, Columbia.

Scarnecchia, D. L., T. W. Gengerke, and C. T. Moen. 1990. Rationale for a harvest slot limit for paddlefish (Polyodon spathula) on the Upper Mississippi River. North American Journal of Fisheries Management. In Press.

Schnick, R. A., J. M. Morton, J. C. Mochalski, and J. T. Beall. 1982. Mitigation and enhancement techniques for the Upper Mississippi River system and other large river systems. United States Fish and Wildlife Service Resource Publication 149, Washington, D. C.

Sheaffer, W. A. 1984. Importance of backwater area confluences to the fishes and macroinvertebrates of the Upper Mississippi River, Pool 13. Master of Science Thesis. Iowa State University, Ames.

Southall, P. D. 1982. Paddlefish movement and habitat use in the Upper Mississippi River. Master of Science Thesis. Iowa State University, Ames.

Southall, P. D., and W. A. Hubert. 1984. Habitat use by adult paddlefish in the Upper Mississippi River. Transactions of the American Fisheries Society 113(2):125-131.

Sparrowe, R. D. 1986. Threats to paddlefish habitat. Pages 36-45 in J. G. Dillard, L. K. Graham, and T. R. Russell, editors. The paddlefish: status, management and propagation. American Fisheries Society, North Central Division, Special Publication 7, Bethesda, Maryland.

Stockard, C. R. 1907. Observations on the natural history of Polyodon spathula. American Naturalist 41:753-766.

Thompson, D. H. 1933. The finding of very young Polyodon. Copeia 1933(1):31-33.

Unkenholz, D. G. 1982. Paddlefish spawning movements and reproductive success in the Missouri River below Fort Randall Dam, 1979-81. South Dakota Department of Game, Fish, and Parks, Progress Report 82-3, Pierre.

Unkenholz, D. G. 1986. Effects of dams and other habitat alterations on paddlefish sport fisheries. Pages 54-61 in J. G. Dillard, L. K. Graham, and T. R. Russell, editors. The paddlefish: status, management and propagation. American Fisheries Society, North Central Division, Special Publication 7, Bethesda, Maryland.

U. S. Army Corps of Engineers. 1980. Upper Mississippi River basin: Mississippi River nine-foot channel navigation project, reservoir regulation manual Appendix 12, Lock and Dam No. 12. United States Army Corps of Engineers, Rock Island, Illinois.

U. S. Army Corps of Engineers. 1982. Upper Mississippi River navigation charts. United States Army Corps of Engineers, North Central Division, Chicago, Illinois.

Wagner, G. 1908. Notes on the fish fauna of Lake Pepin. Transactions of the Wisconsin Academy of Science 16:23-37.

Winter, J. D. 1983. Underwater biotelemetry. Pages 371-395 in L. A. Nielsen and D. L. Johnson, editors. Fisheries Techniques. American Fisheries Society, Bethesda, Maryland.

APPENDIX: MOVEMENTS OF 28 RADIO-TAGGED PADDLEFISH DURING MARCH TO NOVEMBER 1988 IN THE UPPER MISSISSIPPI RIVER (horizontal lines represent Lock and Dam 12 (L&D 12) and Lock and Dam 13 (L&D 13) and River Mile indicates the distance along the main channel upstream from the confluence of the Ohio River at Cairo, Illinois)

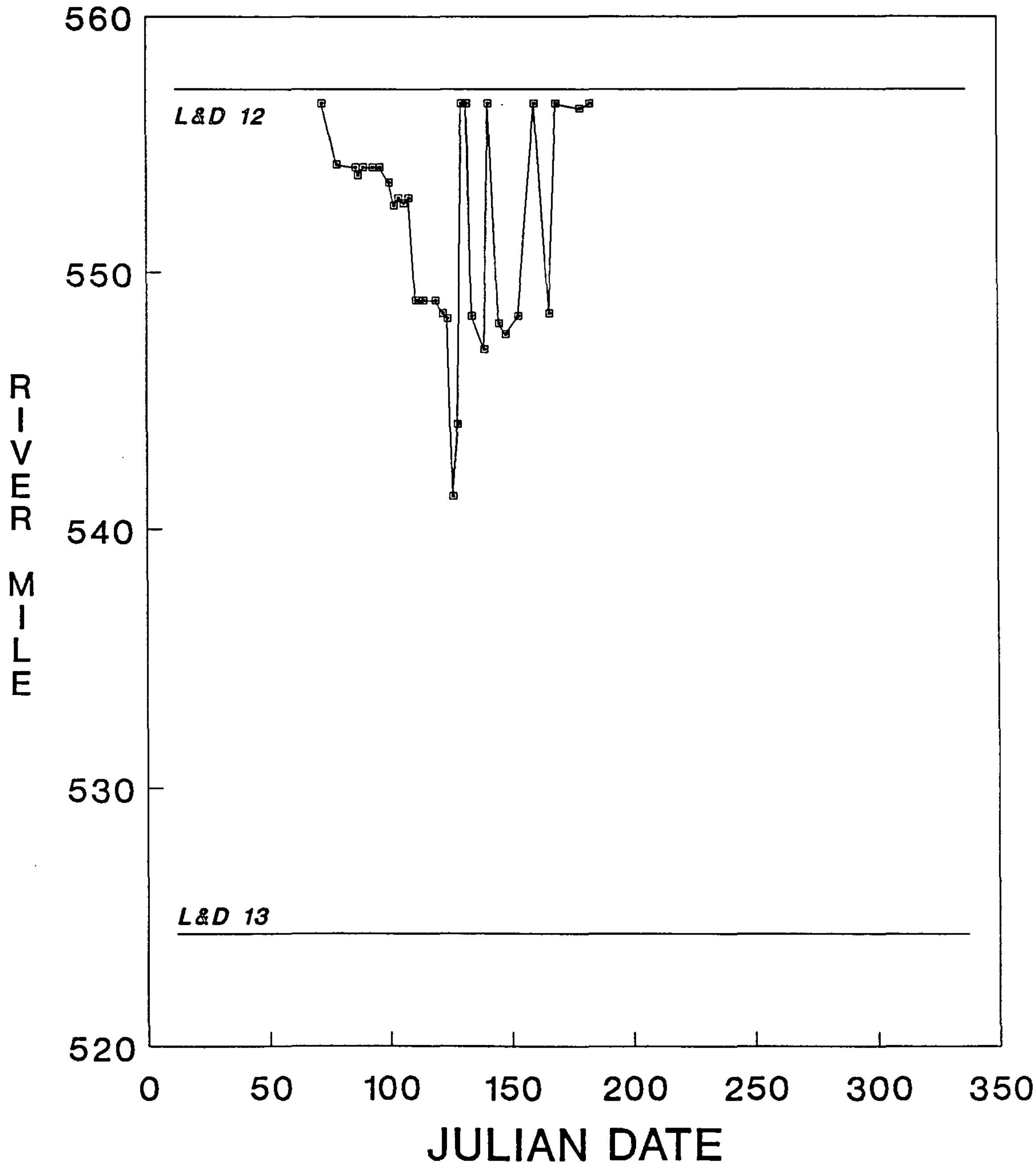


Figure A1. Movement by immature male paddlefish No. 376 during 1988 in the Upper Mississippi River (33 contacts)

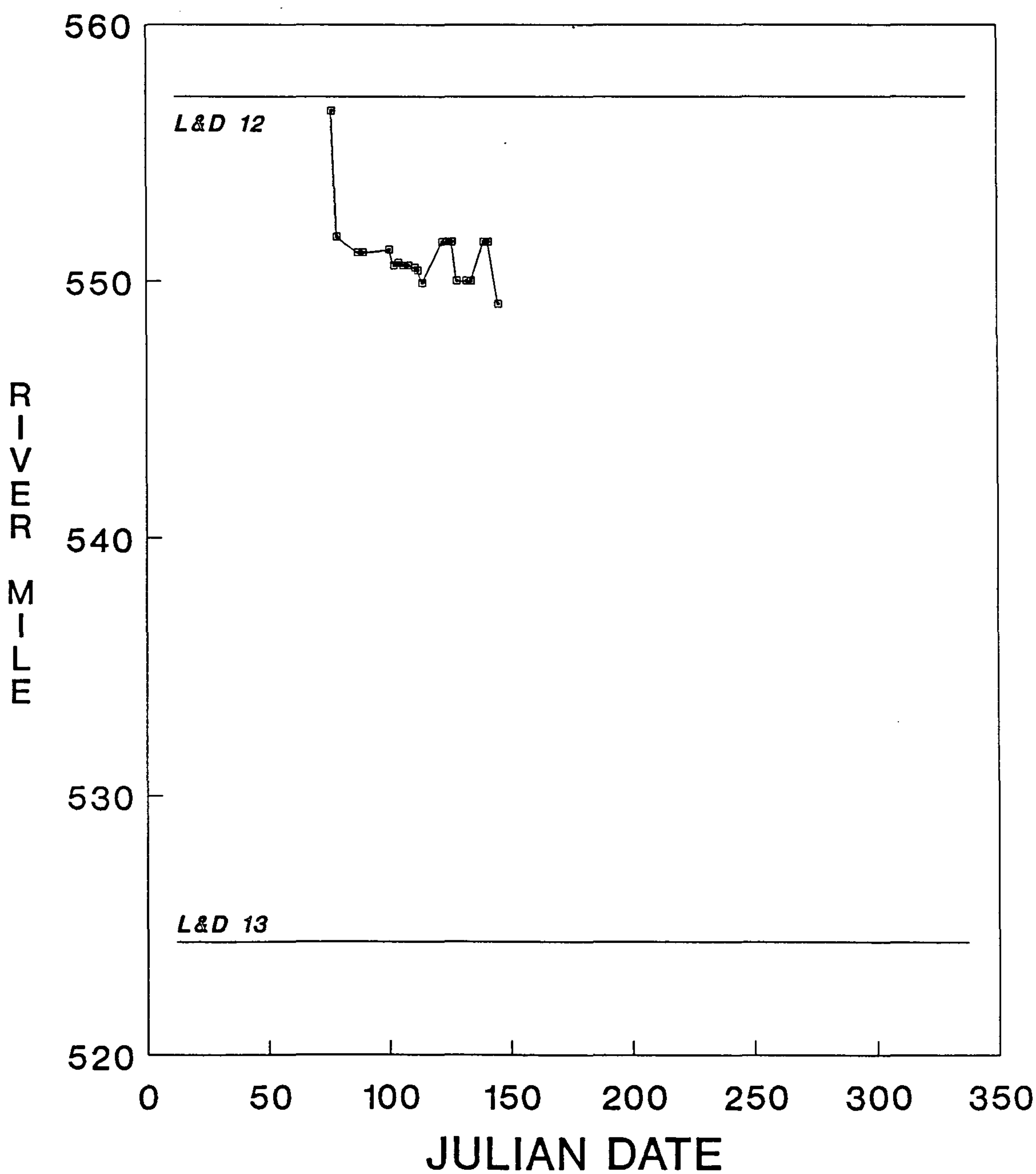


Figure A2. Movement by immature male paddlefish No. 426 during 1988 in the Upper Mississippi River (21 contacts)

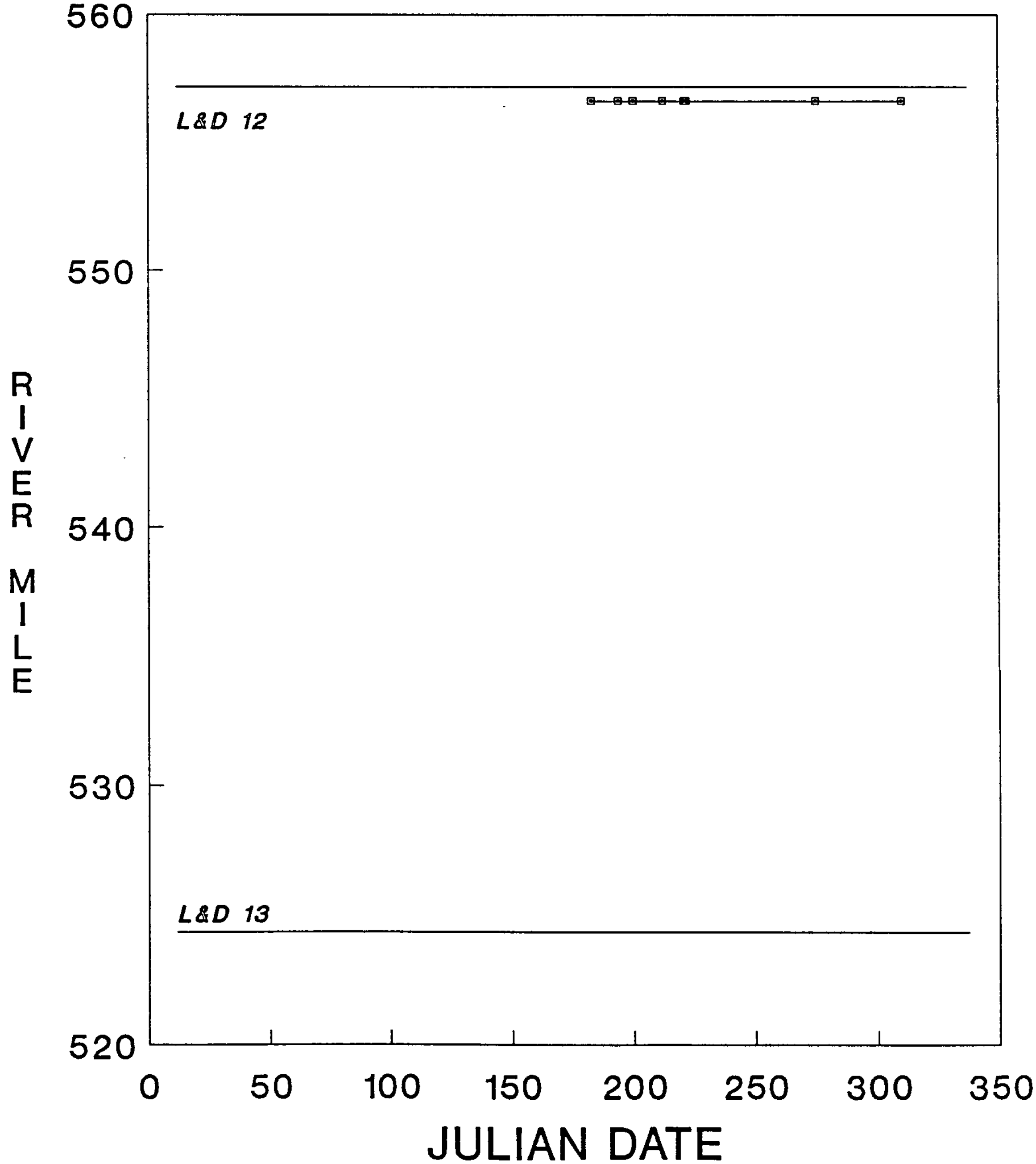


Figure A3. Movement by mature male paddlefish No. 59 during 1988 in the Upper Mississippi River (8 contacts)

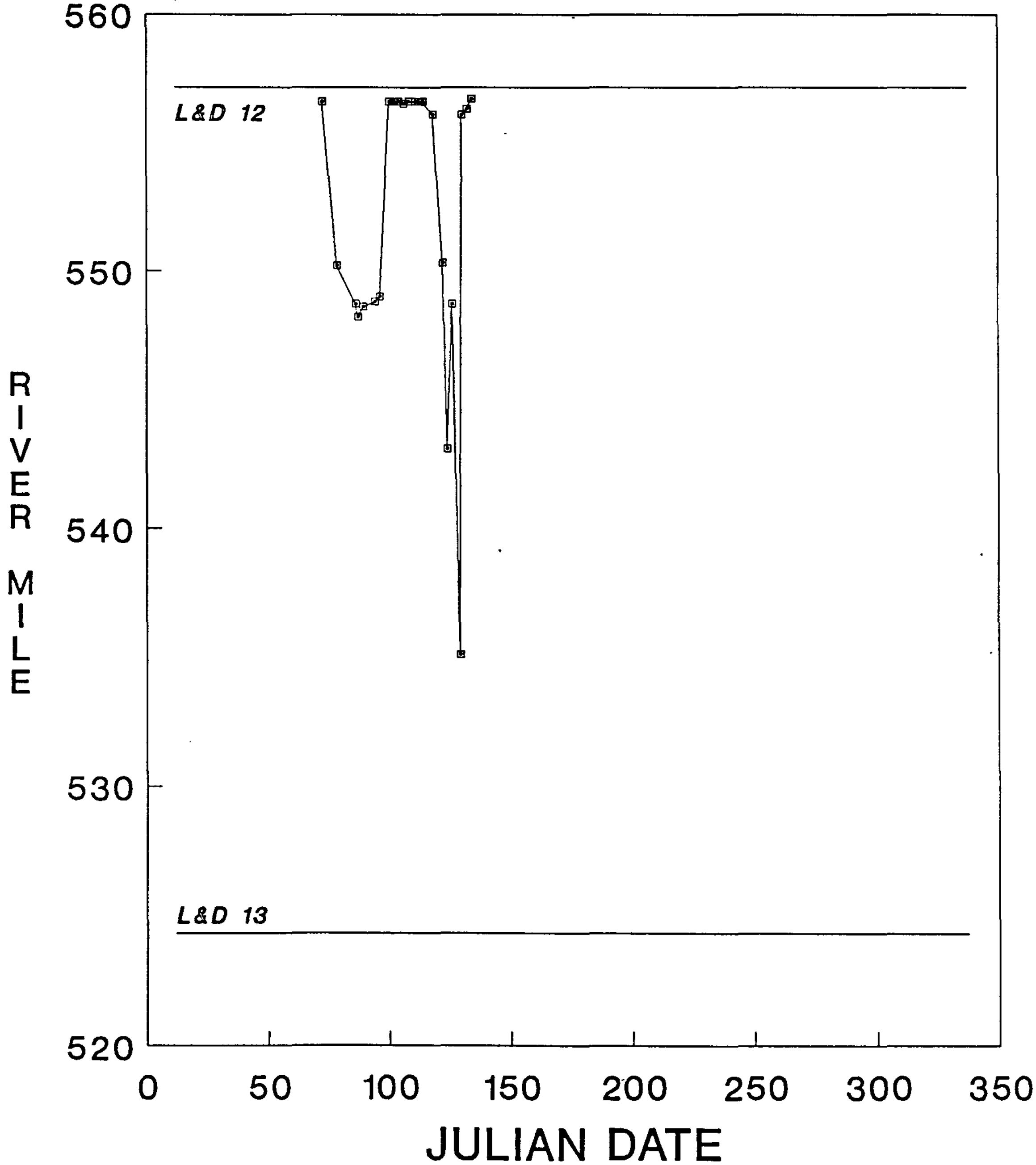


Figure A4. Movement by mature male paddlefish No. 78 during 1988 in the Upper Mississippi River (24 contacts)

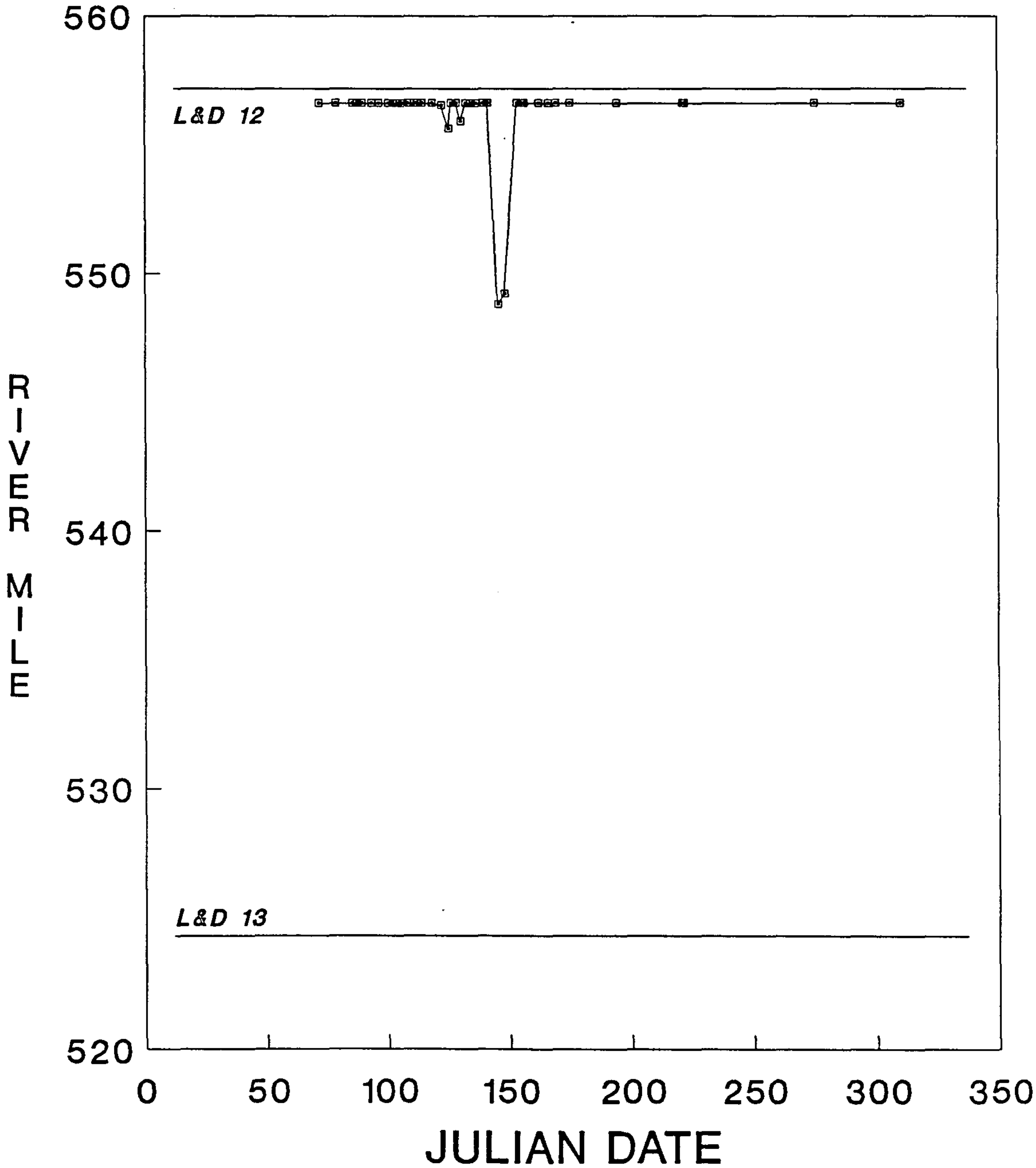


Figure A5. Movement by mature male paddlefish No. 116 during 1988 in the Upper Mississippi River (41 contacts)

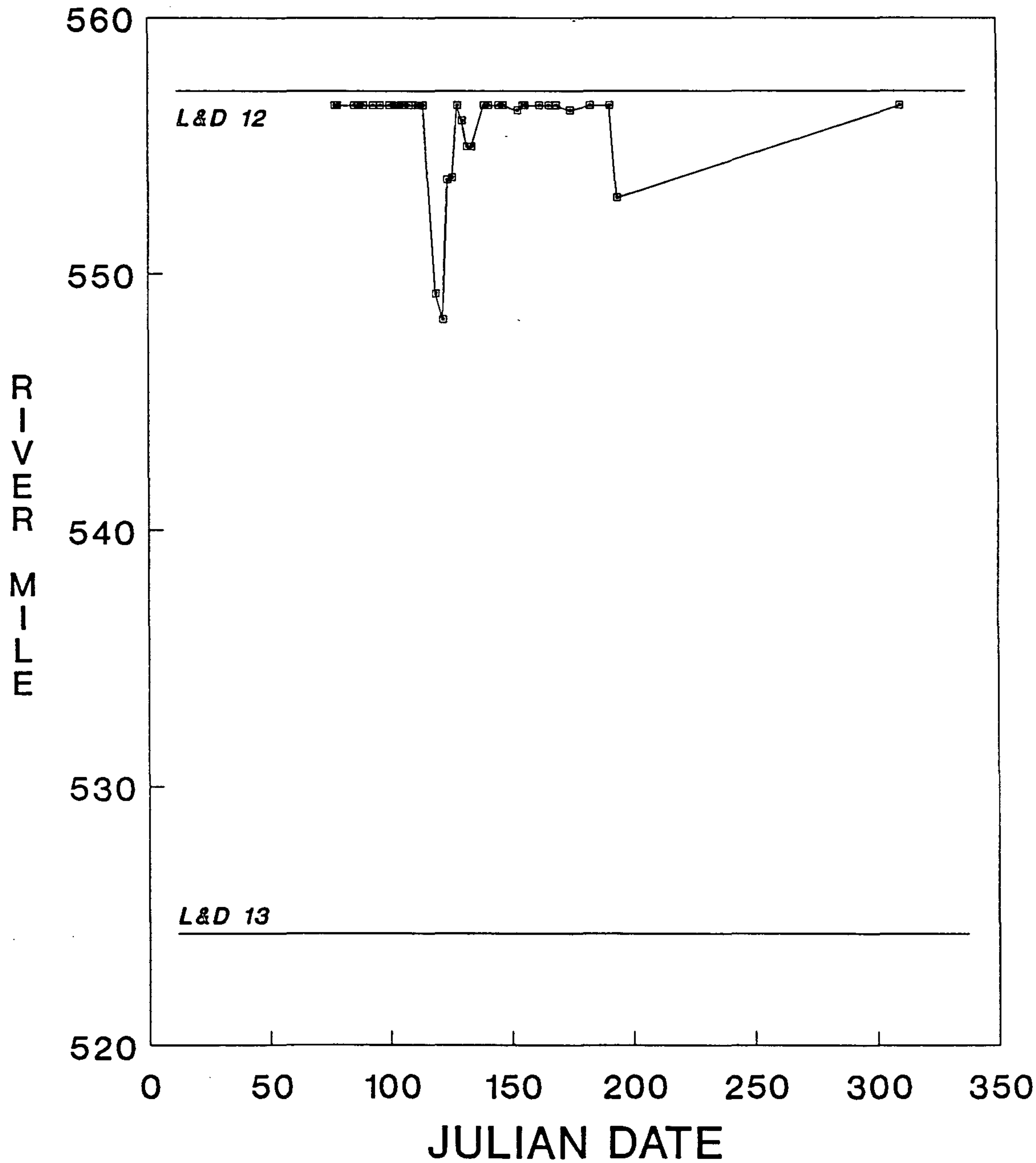


Figure A6. Movement by mature male paddlefish No. 128 during 1988 in the Upper Mississippi River (38 contacts)

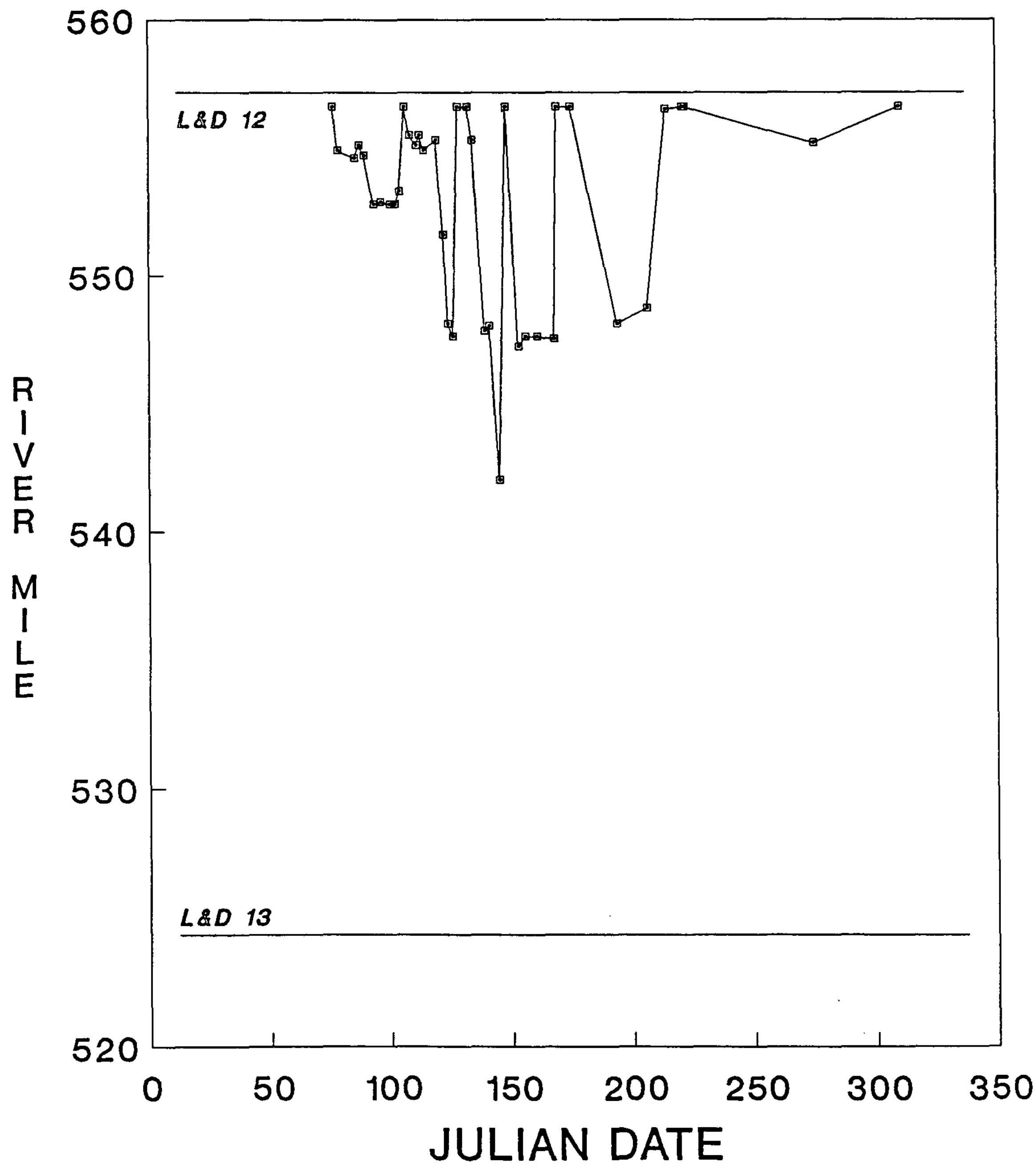


Figure A7. Movement by mature male paddlefish No. 239 during 1988 in the Upper Mississippi River (39 contacts)

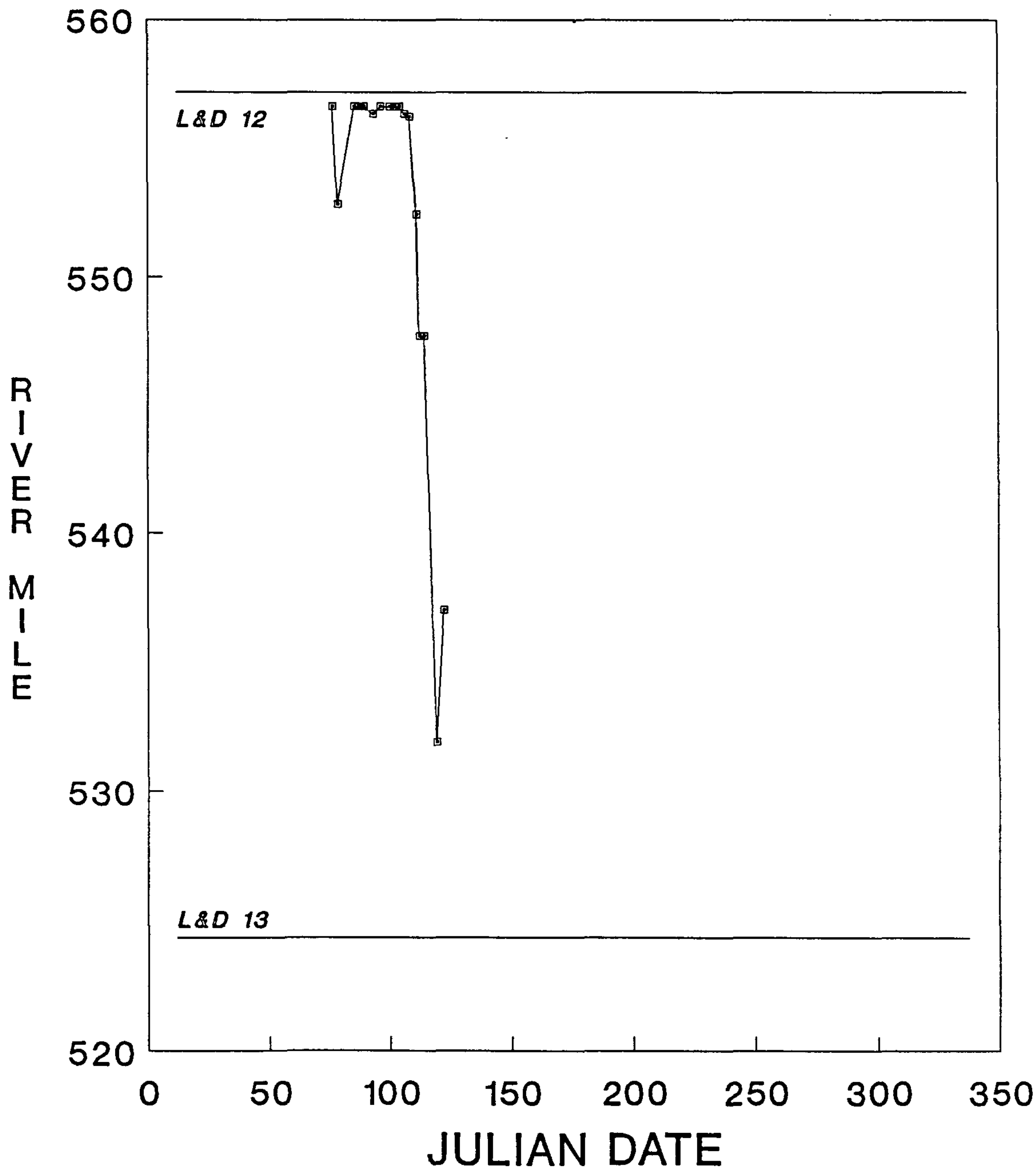


Figure A8. Movement by immature female paddlefish No. 148 during 1988 in the Upper Mississippi River (17 contacts)

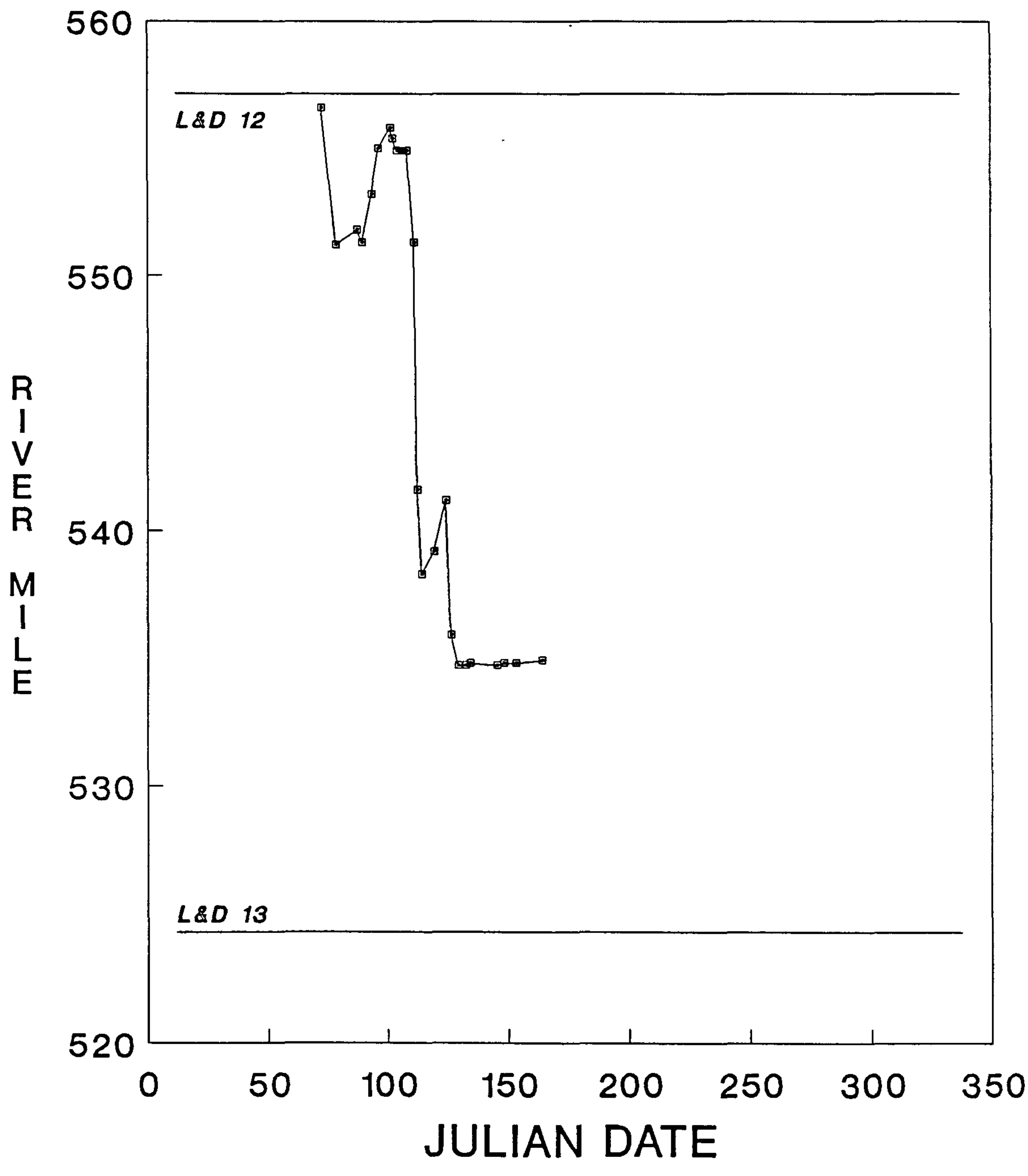


Figure A9. Movement by immature female paddlefish No. 349 during 1988 in the Upper Mississippi River (24 contacts)

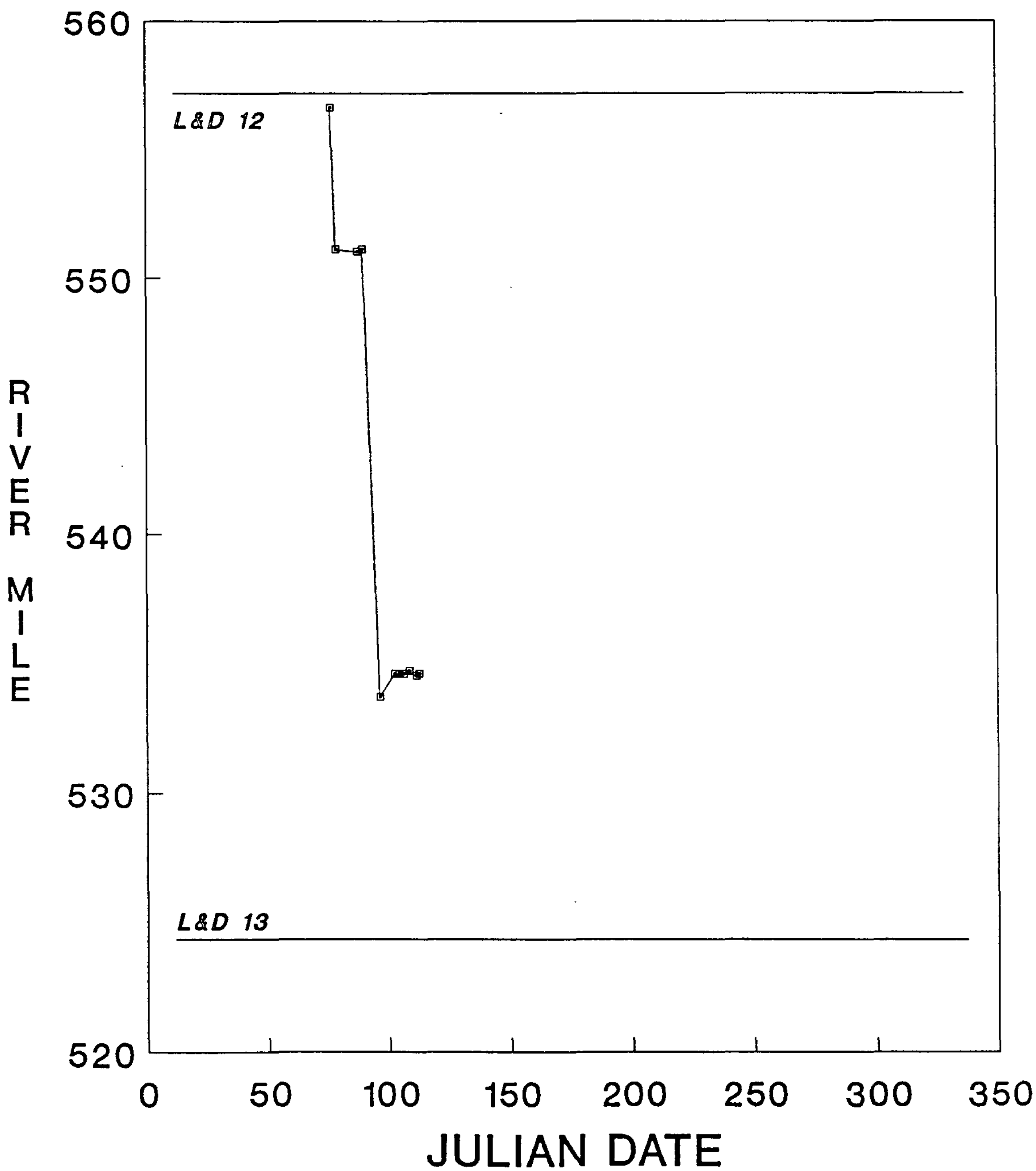


Figure A10. Movement by immature female paddlefish No. 367 during 1988 in the Upper Mississippi River (11 contacts)

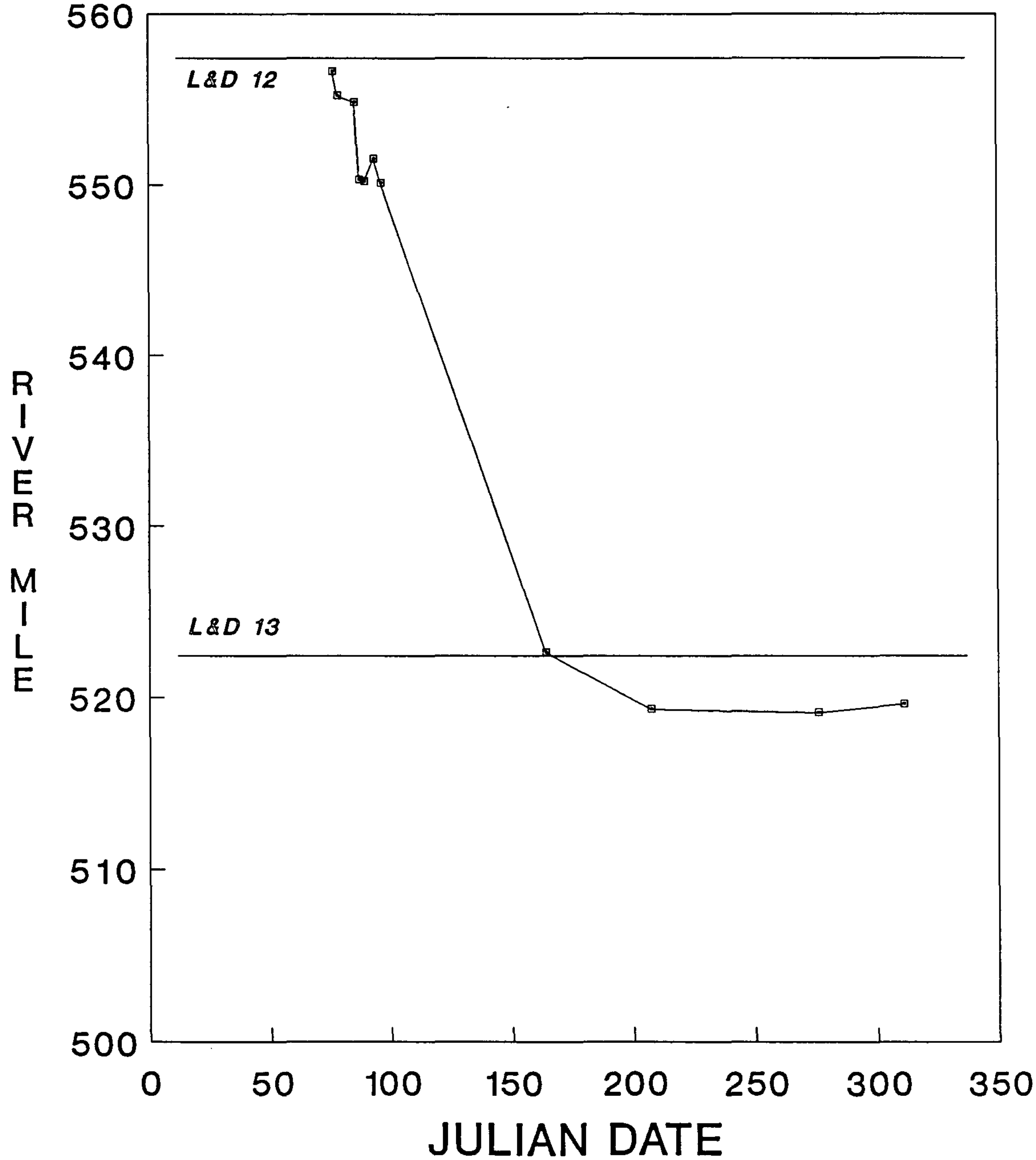


Figure A11. Movement by maturing female paddlefish No. 39 during 1988 in the Upper Mississippi River (12 contacts)

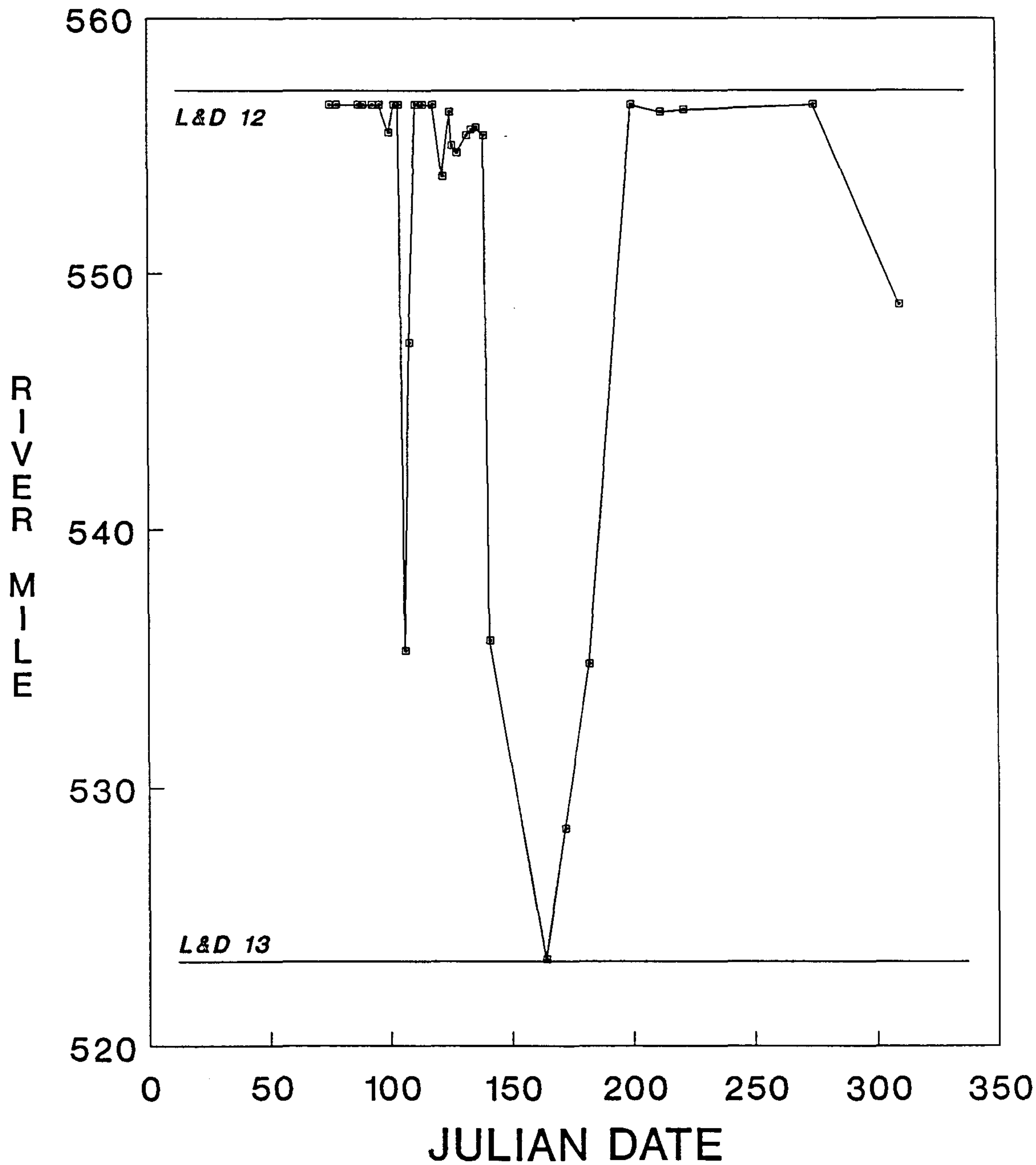


Figure A12. Movement by maturing female paddlefish No. 158 during 1988 in the Upper Mississippi River (32 contacts)

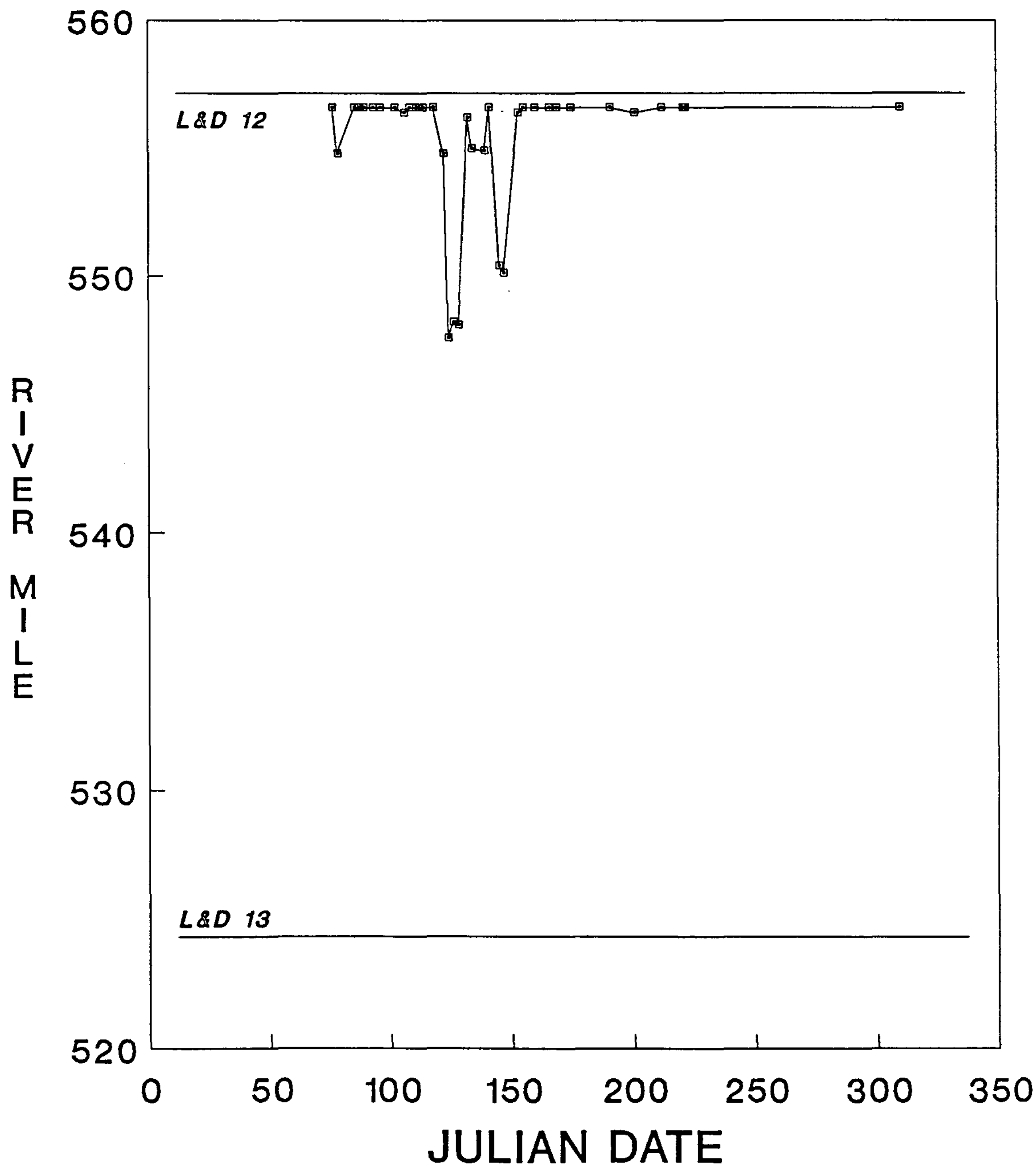


Figure A13. Movement by maturing female paddlefish No. 218 during 1988 in the Upper Mississippi River (36 contacts)

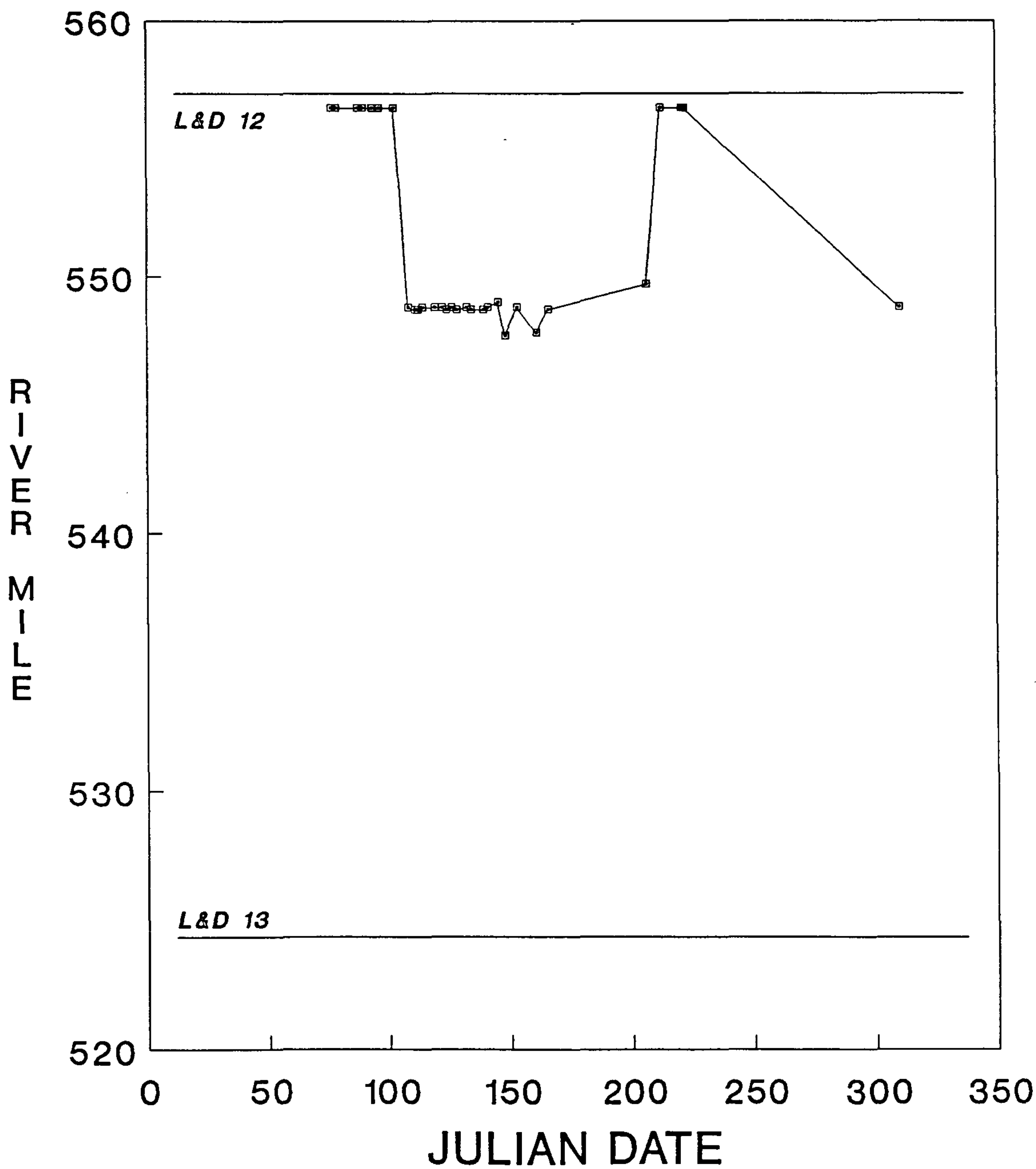


Figure A14. Movement by maturing female paddlefish No. 257 during 1988 in the Upper Mississippi River (31 contacts)

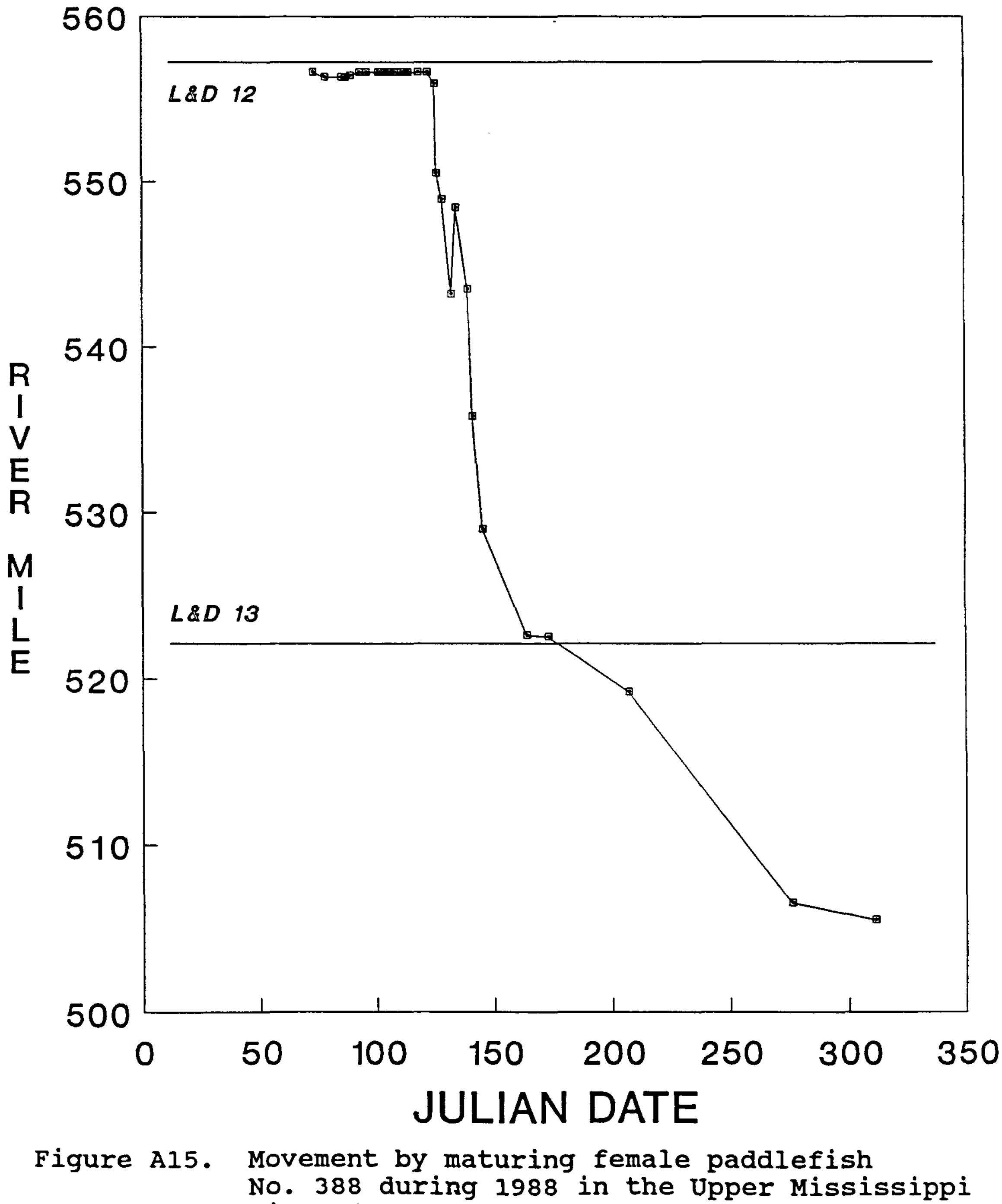


Figure A15. Movement by maturing female paddlefish No. 388 during 1988 in the Upper Mississippi River (29 contacts)

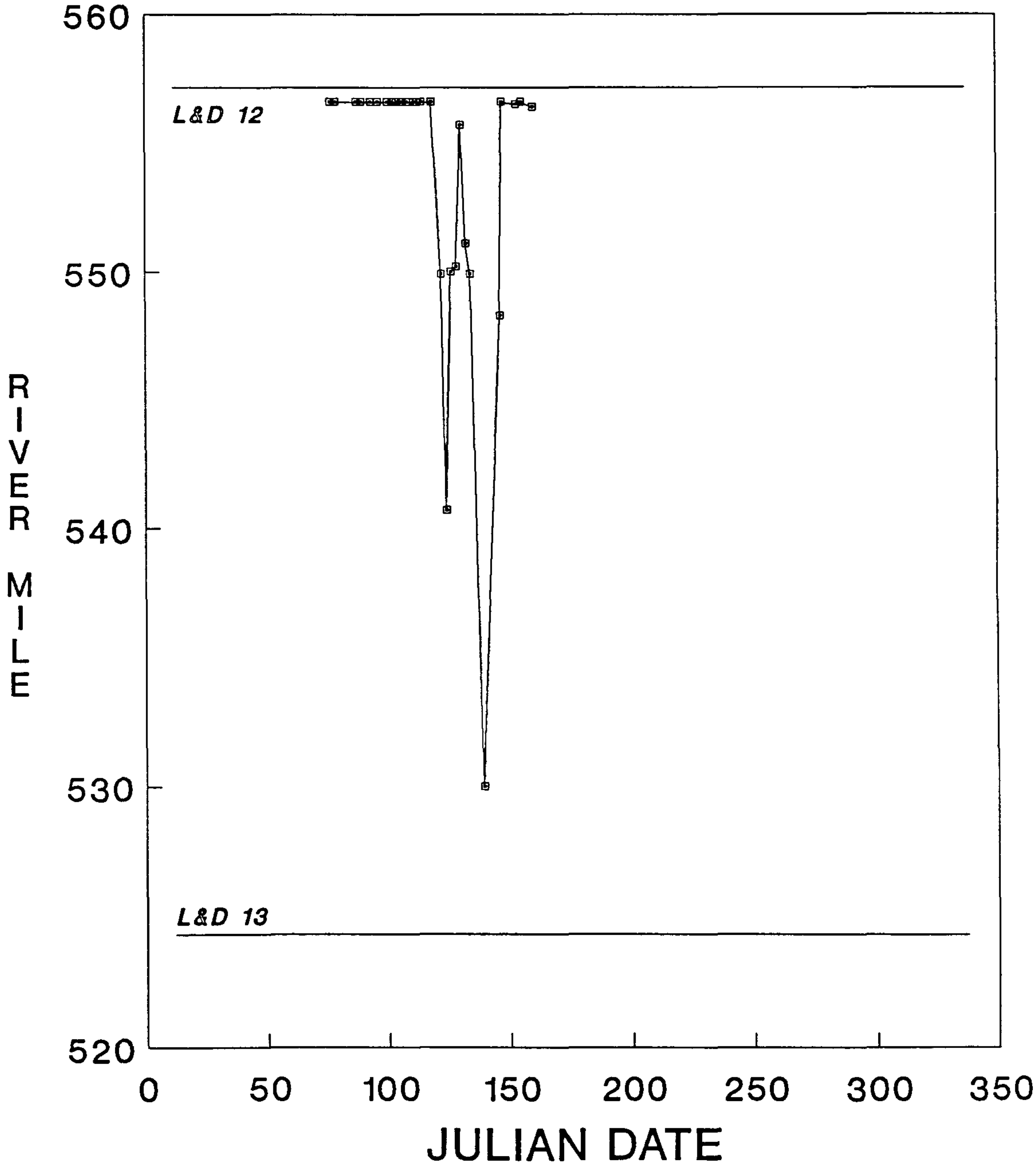


Figure A16. Movement by maturing female paddlefish No. 419 during 1988 in the Upper Mississippi River (29 contacts)

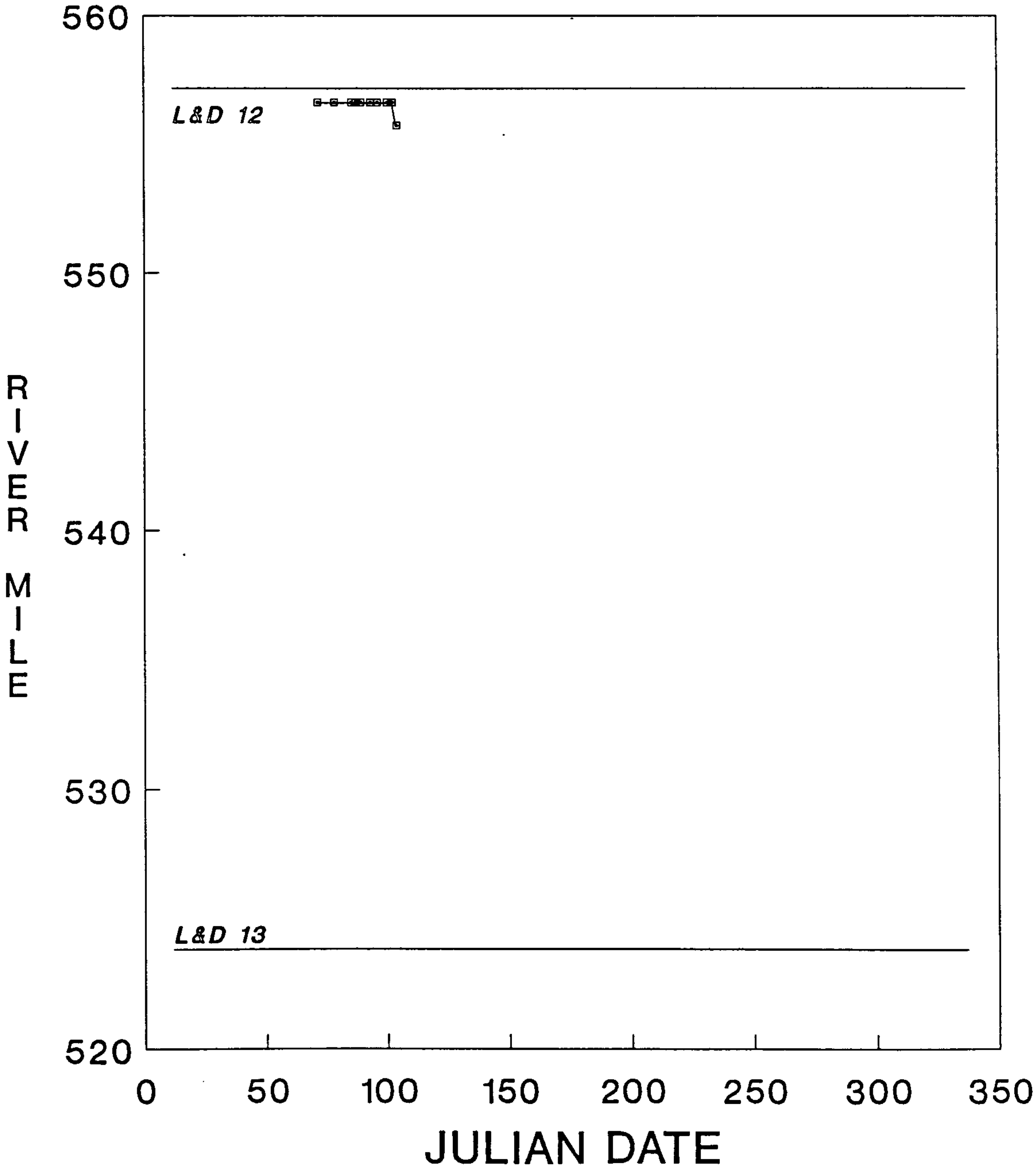


Figure A17. Movement by mature female paddlefish No. 59 during 1988 in the Upper Mississippi River (10 contacts)

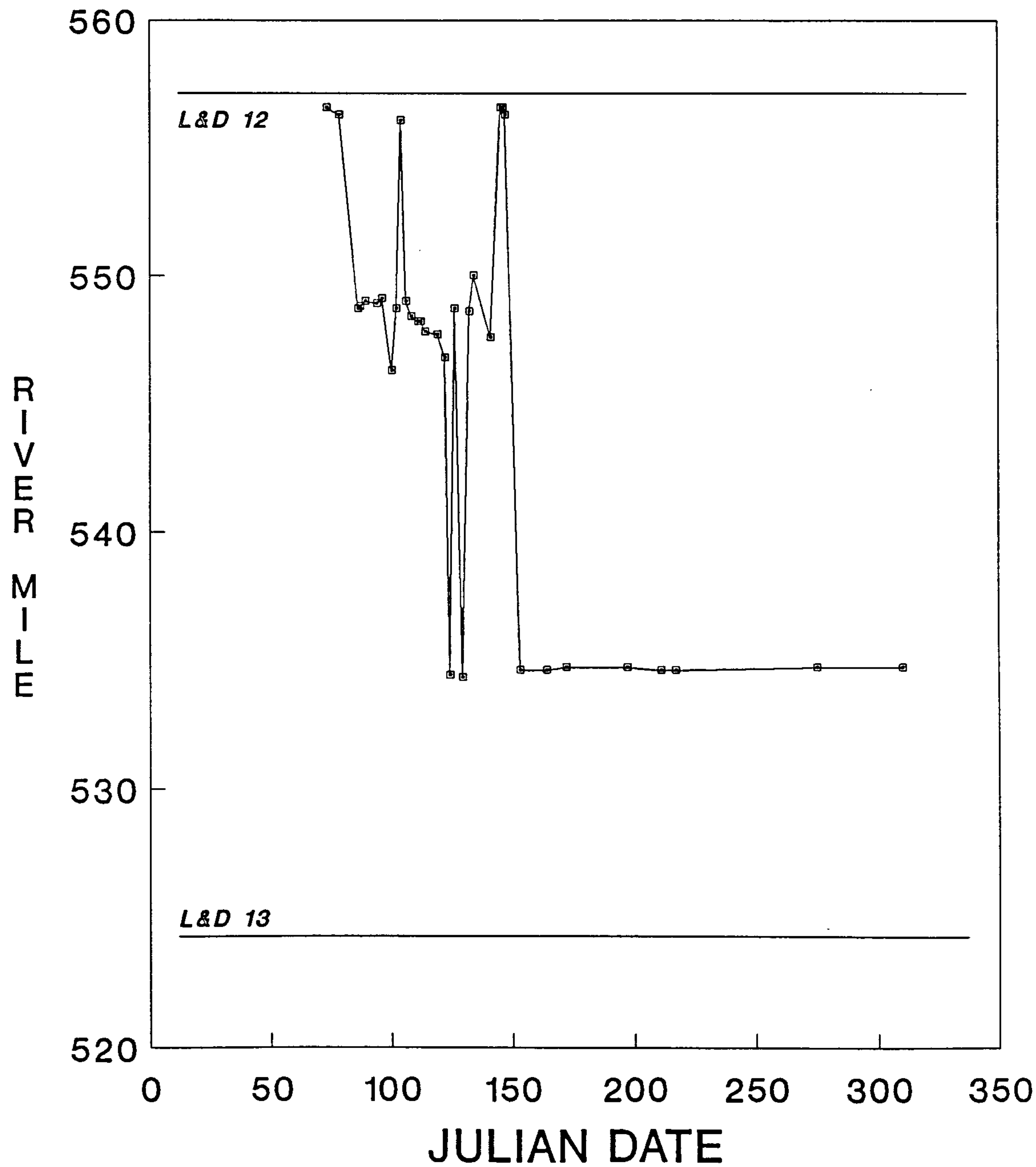


Figure A18. Movement by mature female paddlefish No. 86 during 1988 in the Upper Mississippi River (34 contacts)

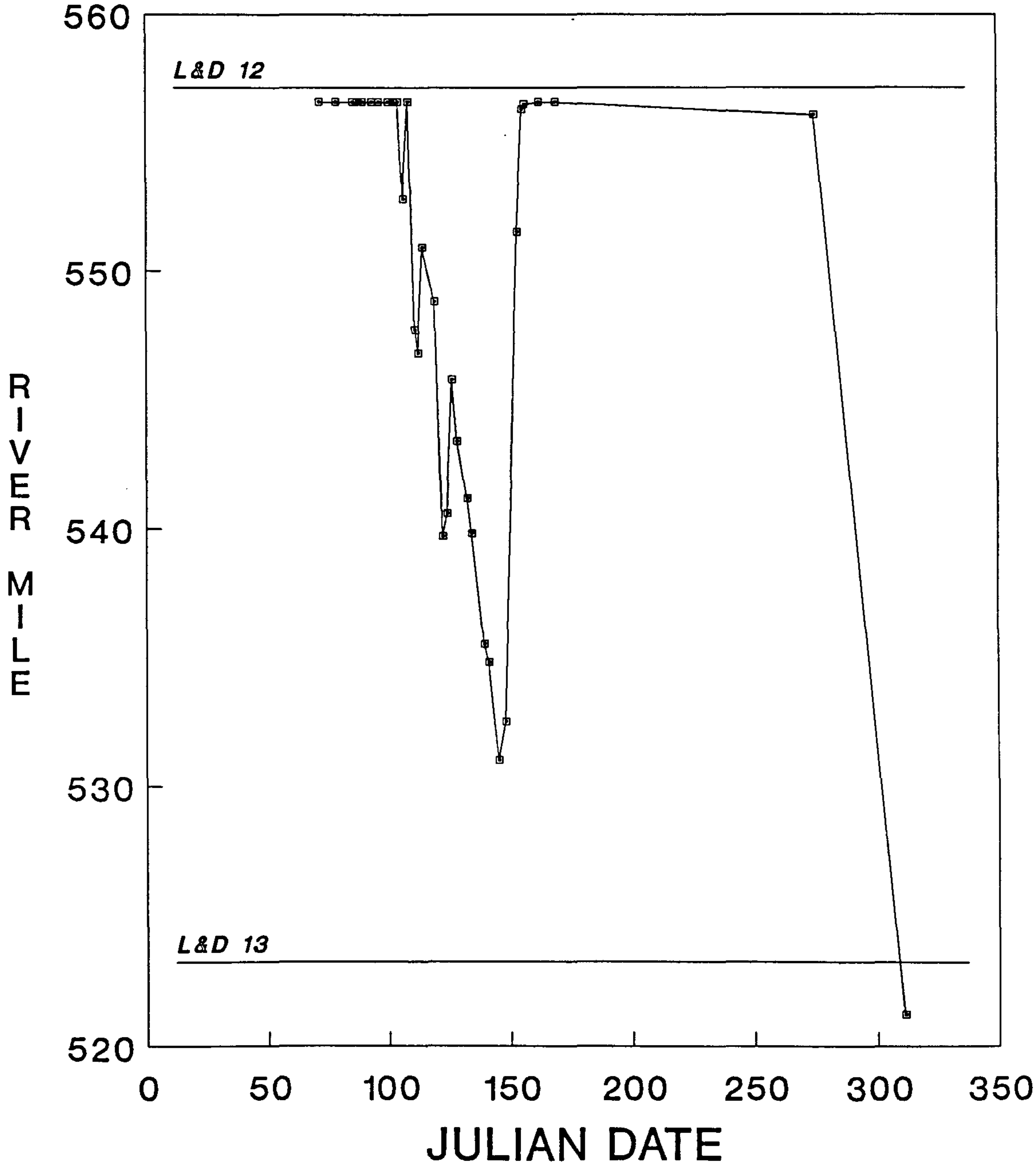


Figure A19. Movement by mature female paddlefish No. 108 during 1988 in the Upper Mississippi River (33 contacts)

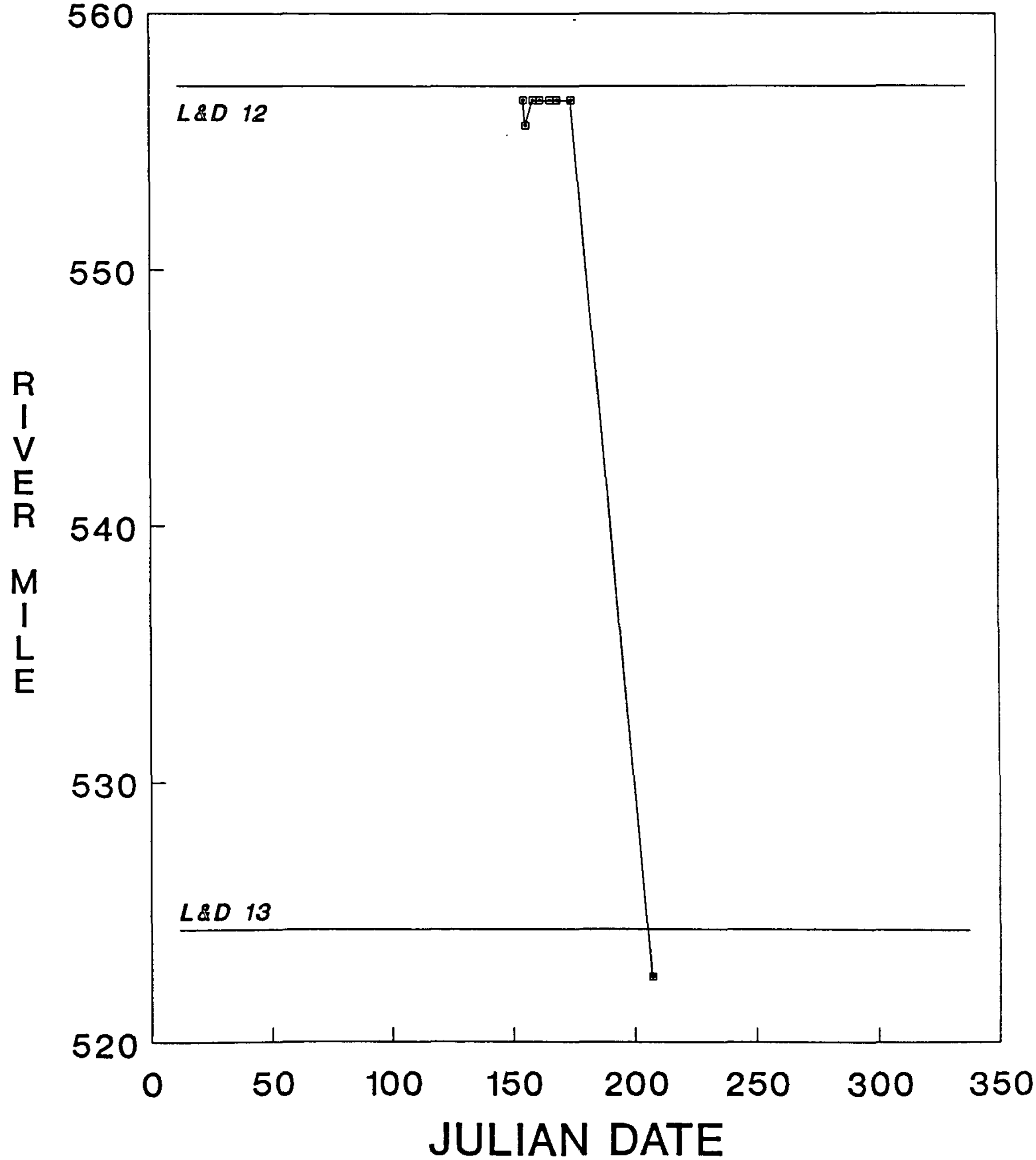


Figure A20. Movement by mature female paddlefish No. 148 during 1988 in the Upper Mississippi River (8 contacts)

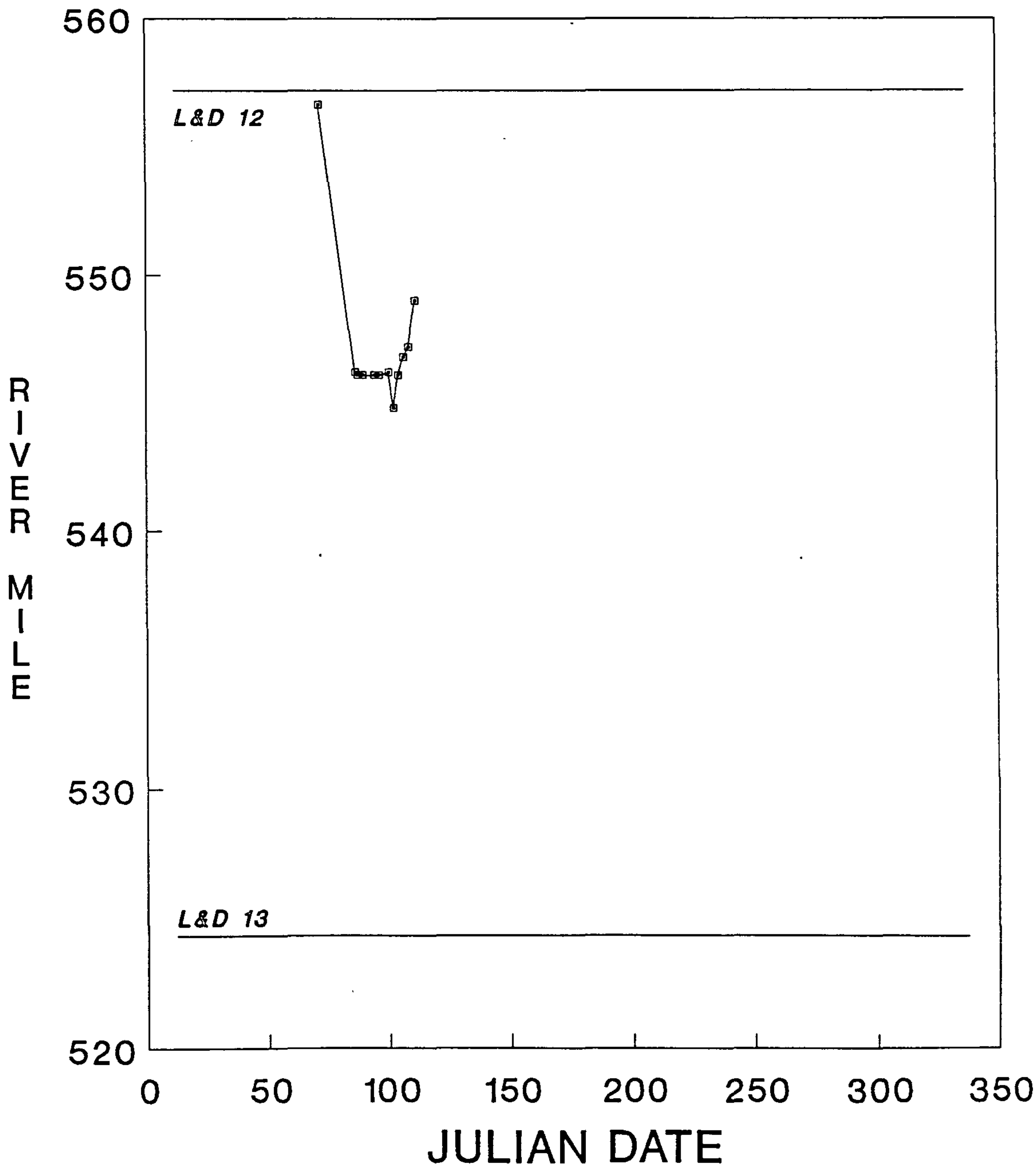


Figure A21. Movement by mature female paddlefish No. 168 during 1988 in the Upper Mississippi River (12 contacts)

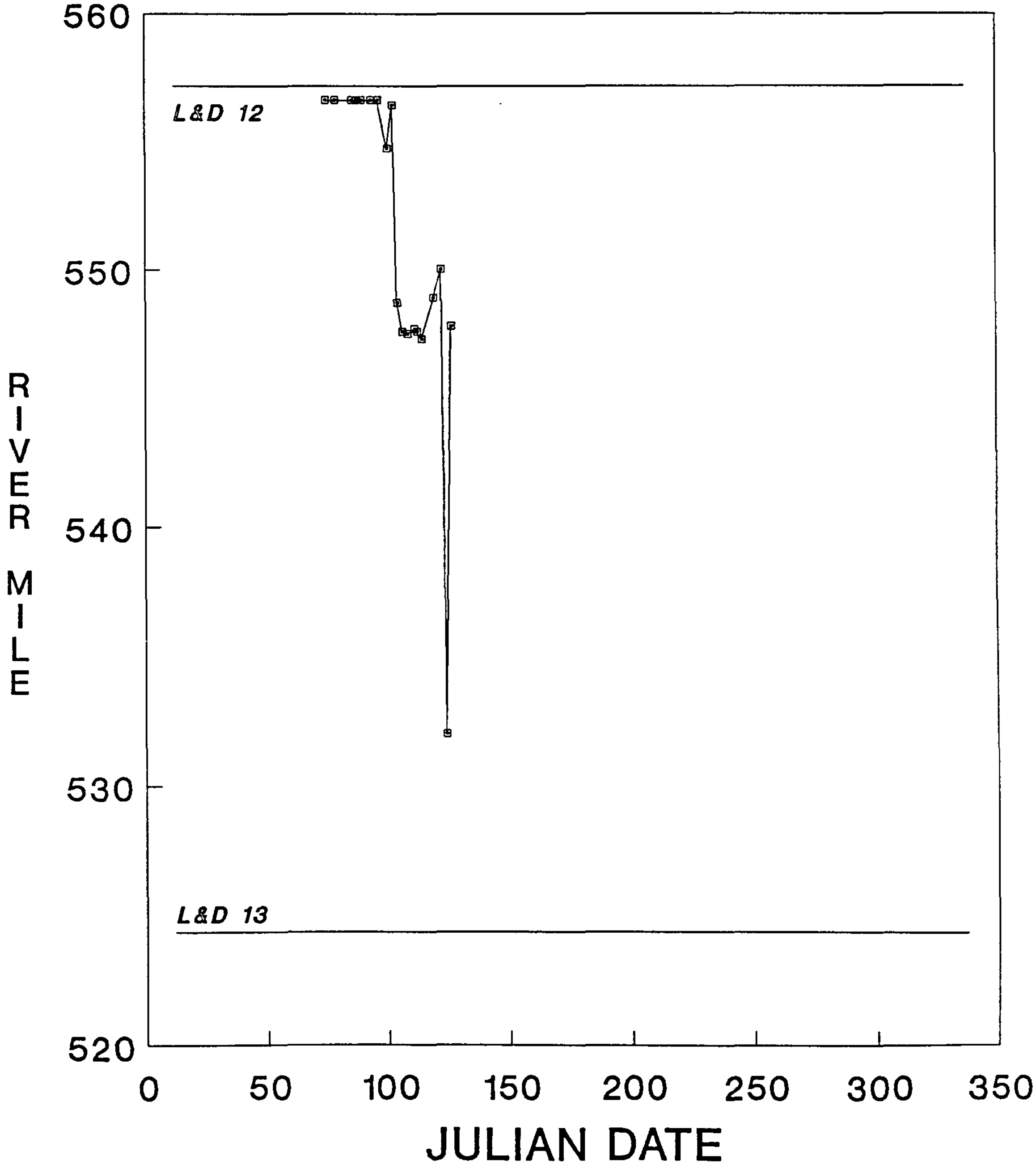


Figure A22. Movement by mature female paddlefish No. 179 during 1988 in the Upper Mississippi River (19 contacts)

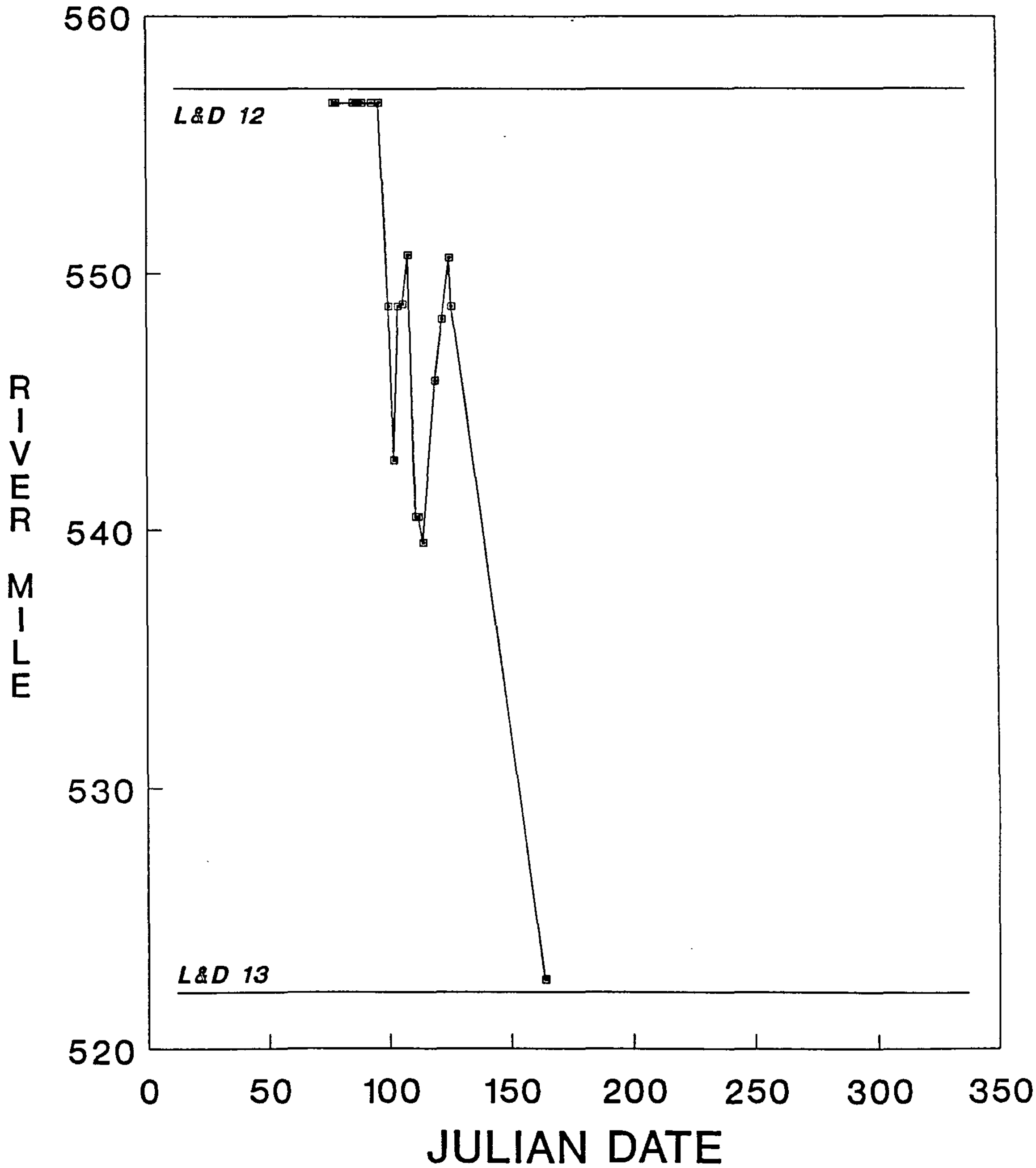


Figure A23. Movement by mature female paddlefish No. 188 during 1988 in the Upper Mississippi River (20 contacts)

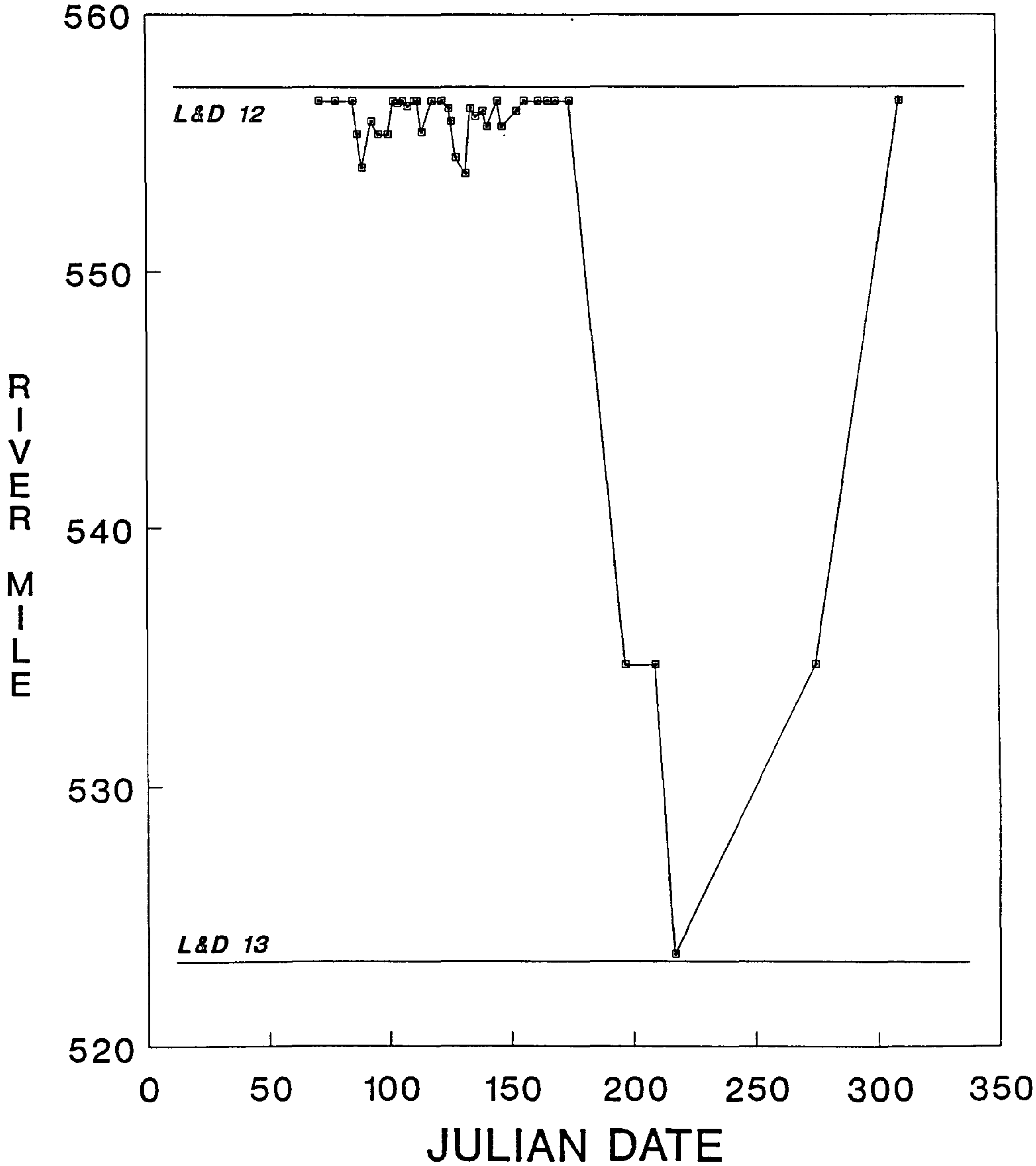


Figure A24. Movement by mature female paddlefish No. 227 during 1988 in the Upper Mississippi River (38 contacts)

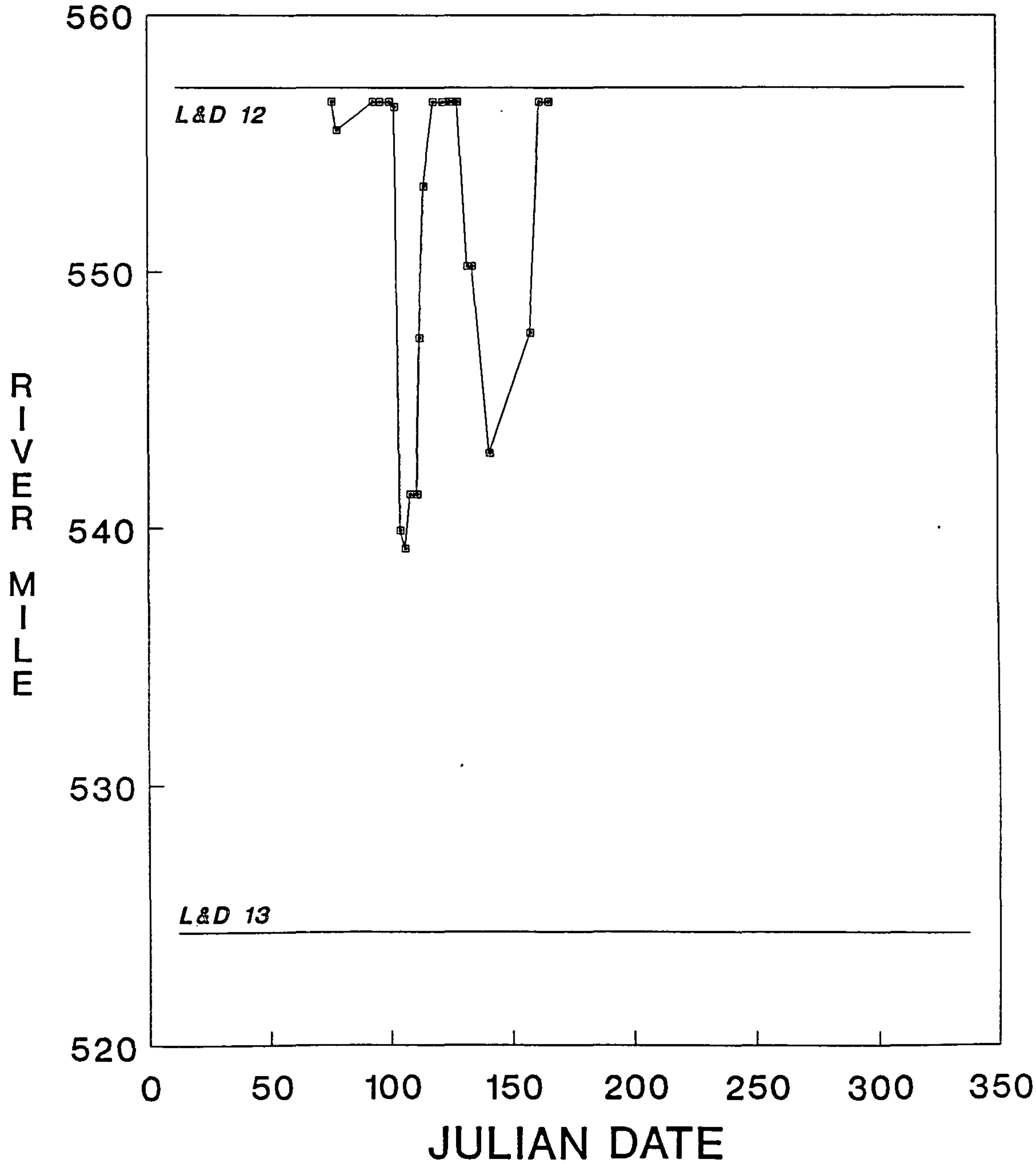


Figure A25. Movement by mature female paddlefish No. 328 during 1988 in the Upper Mississippi River (23 contacts)

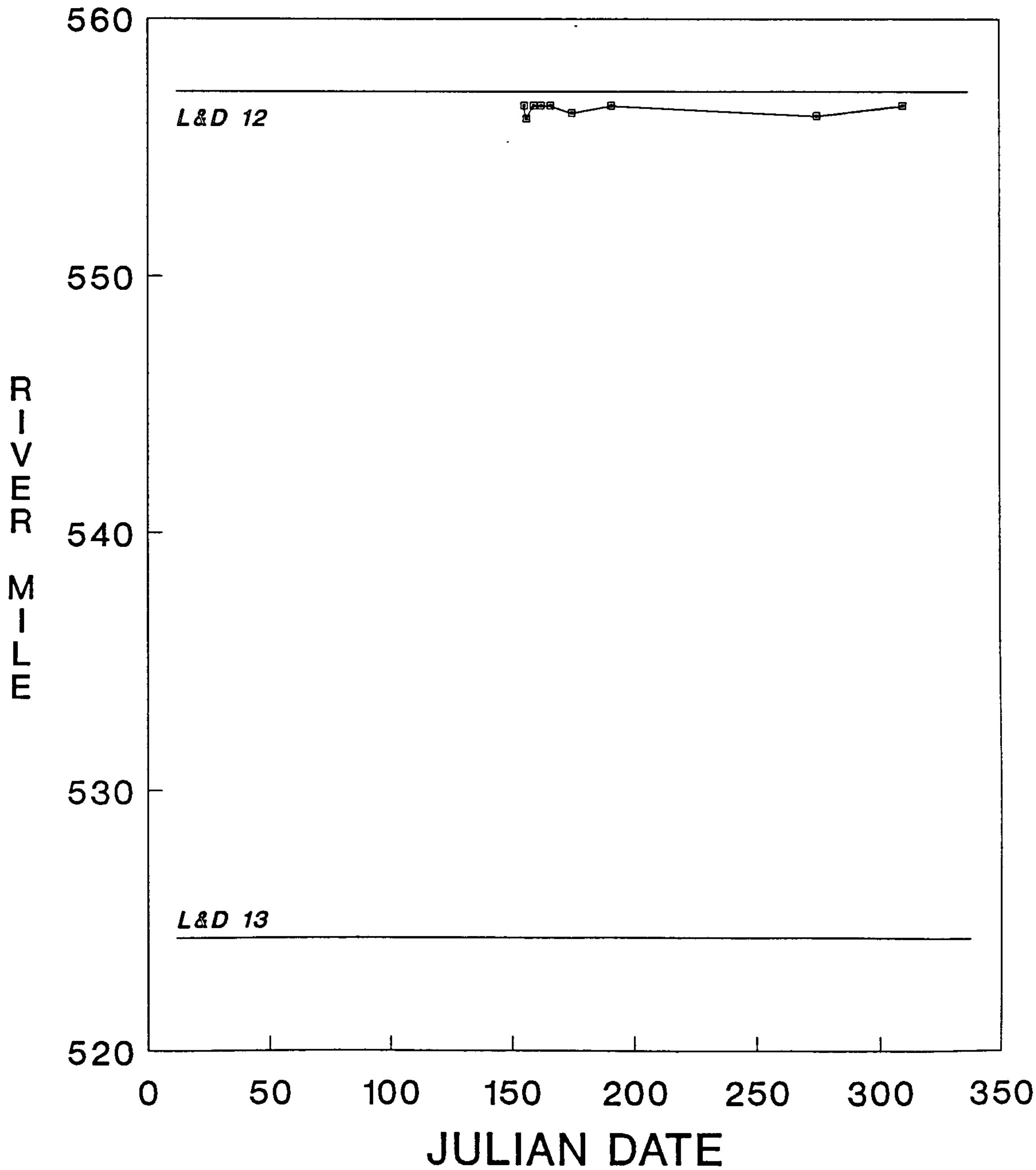


Figure A26. Movement by mature female paddlefish No. 367 during 1988 in the Upper Mississippi River (9 contacts)

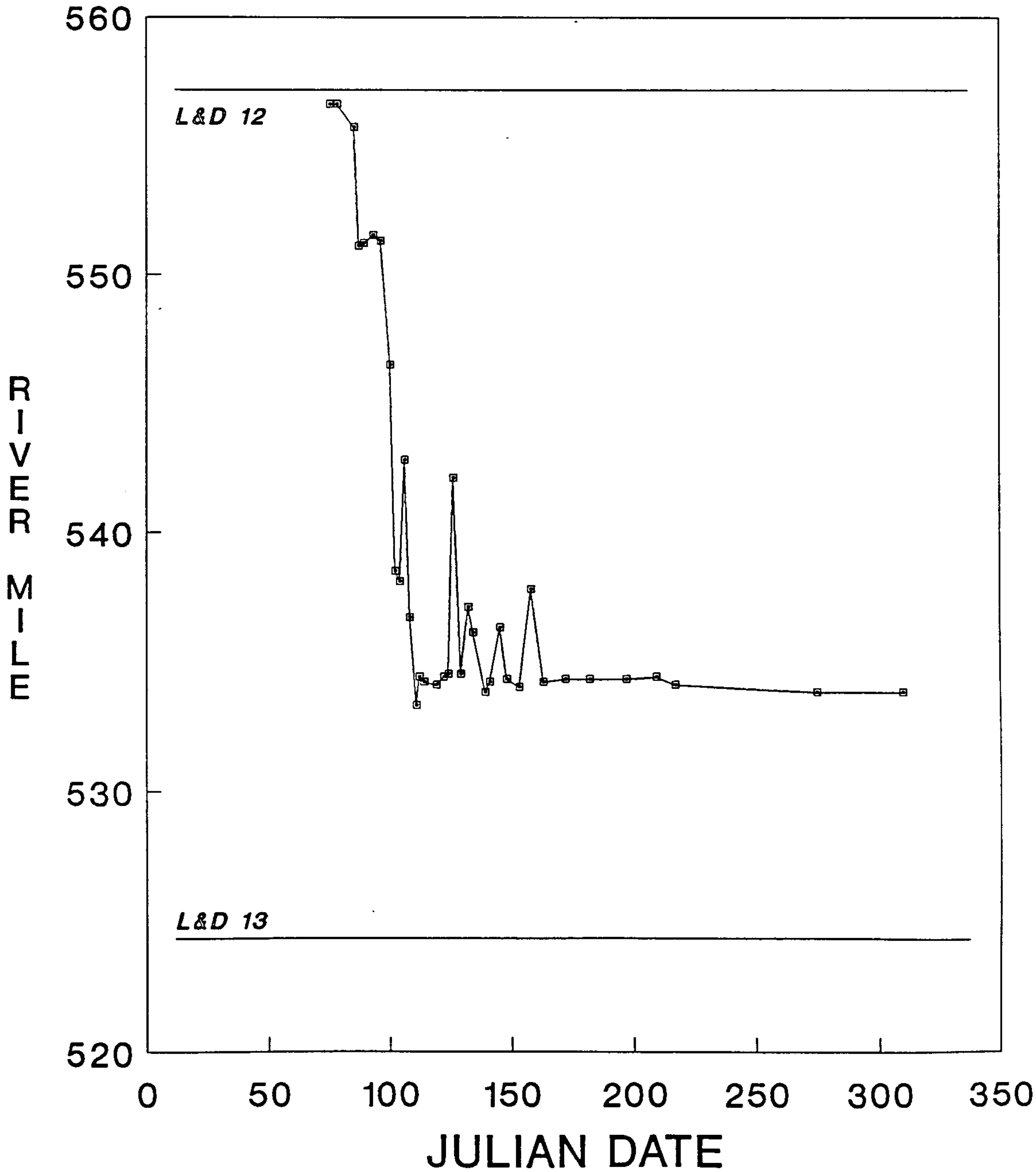


Figure A27. Movement by mature female paddlefish No. 408 during 1988 in the Upper Mississippi River (36 contacts)

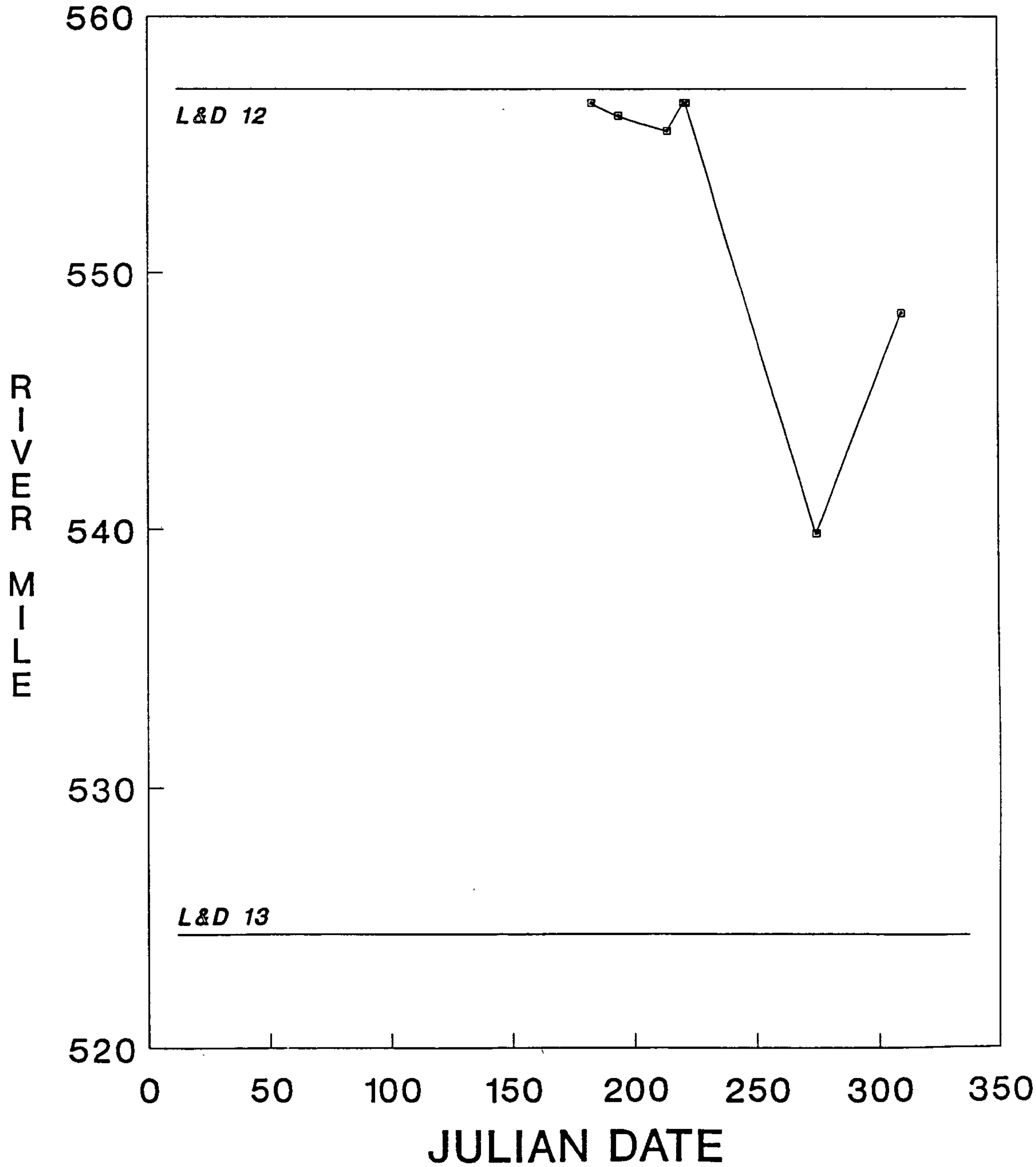


Figure A28. Movement by mature female paddlefish No. 426 during 1988 in the Upper Mississippi River (7 contacts)